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Abstract: This paper examines the hunting strategies employed by Neanderthals at a series of kill or near-kill sites from the Middle Palaeolithic of Europe (Mauran, La Borde, Taubach, Zwolen and Salzgitter Lebenstedt). Using palaeolandscape reconstructions and animal ethology as our context, we adopt a multifaceted approach that views hunting as a chaîne opératoire involving the decisions and actions of both the hunter and the hunted, which together help reconstruct a forensic picture of past events as they unfolded. Our conclusions indicate that Neanderthals did not necessarily pre-select individuals from a herd, who they then isolated, pursued and killed, but rather ambushed whole groups, which they slaughtered indiscriminately. There is strong evidence, however, that Neanderthals were highly selective in the carcasses they then chose to process. Our conclusions suggest that Neanderthals were excellent tacticians, casual executioners and discerning diners.

Shoot First, Ask Questions Later: interpretative narratives of Neanderthal hunting.

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Abstract

This paper examines the hunting strategies employed by Neanderthals at a series of kill or near-kill sites from the Middle Palaeolithic of Europe (Mauran, La Borde, Taubach, Zwoleń and Salzgitter Lebenstedt). Using palaeolandscape reconstructions and animal ethology as our context, we adopt a multifaceted approach that views hunting as a chaîne opératoire involving the decisions and actions of both the hunter and the hunted, which together help reconstruct a forensic picture of past events as they unfolded. Our conclusions indicate that Neanderthals did not necessarily pre-select individuals from a herd, who they then isolated, pursued and killed, but rather ambushed whole groups, which they slaughtered indiscriminately. There is strong evidence, however, that Neanderthals were highly selective in the carcasses they then chose to process. Our conclusions suggest that Neanderthals were excellent tacticians, casual executioners and discerning diners.

Introduction: The Genuine Palaeodiet

The reconstruction of Neanderthal diet is currently undergoing something of a revolution. In addition to traditional methods of archaeozoological analysis of Middle Palaeolithic faunal assemblages, supplemented since the mid 1990s by the isotopic analysis of Neanderthal remains (Drucker and Bocherens 2004. Bocherens et al. 2001, 2005; Richards et al. 2000, 2001; Richards and Trinkaus 2009), identifications of animal and plant residues on Neanderthal teeth and Middle Palaeolithic stone tools are now being rolled out (Hardy et al. 2012; Henry et al 2011). A picture is emerging of regional dietary variability (Bar-Yosef 2004; Burke 2000; 2004. Steele 2004), with Neanderthals showing sufficient flexibility to exploit locally available animal and plant resources as they became seasonally available (e.g., Stiner 1994; Gaudzinski 1996. 2006), including slow and fast moving small animals (Stiner 2002; Blasco 2008) and lesser, but at times not insignificant, amounts of aquatic, marine, avian and plant elements (Barton 2000; Blaso and Fernández Peris 2009; Hardy and Moncel 2011; Henry et al. 2011; Hardy et al. 2012). Indeed, it now seems clear that in some regions of Europe and during certain seasons Neanderthal diets could be described as broad spectrum, at least in southern Europe (Gaudzinski-Windheuser and Kindler 2012, 62).

This maturing picture builds on two decades of research that saw dramatic changes in our appreciation of Neanderthal hunting. After many years of being characterized as predominantly, if not obligate, scavengers (e.g. Binford 1981, 1984, 1985; Stiner 1991; 1994), Neanderthals have come to be seen as capable hunters, even top-level carnivores, possessing similar capabilities in the hunting realm as *Homo sapiens*. As noted by Gaudzinski-Windheuser and Kindler (2012, 60), the discovery of preserved wooden spears at the late Middle Pleistocene site of Schöningen (Germany) effectively ended a research paradigm in which the ‘hunter or scavenger’ dichotomy was a major issue for debate. It has simply been assumed since that Neanderthals were (or perhaps *could be* is a better term) efficient hunters of large mammals. The abundance of large animal remains and stone tools from over half of the known European Middle Palaeolithic sites, age profiles of taxa present and the ubiquity of cutmarks and other signs of processing of these remains ‘indicate that Middle Palaeolithic humans at times enjoyed uninhibited access to large game, apparently by hunting them’ (Stiner 2002, 17). As Burke succinctly put it, “the issue today is not *whether* Middle Palaeolithic people could hunt, but rather *when* and *how* they chose to hunt” (2000, 281 emphasizes original). Some of the best evidence comes from sites where the faunal assemblage takes a monospecific form – i.e. the record is dominated by a single taxon, often with large numbers of individuals present. These become more common from Marine Oxygen Isotope Stage (MIS)9 or MIS7 onwards and particularly from MIS5e (Gaudzinski 1996. 1999a. 2006; papers in Burke 2000 and 2004; Rodriguez-Hidalgo et al., 2015). The taxa involved are diverse and include equids (Conard and Prindiville 2000., Patou-Mathis 2004, Schild et al 2006), rhinoceros (Bratlund 1999), reindeer (Gaudzinski and Roebroeks 2000), bovids (Farizy et al 1994; Jaubert et al 1990; Gaudzinski 1996. 2006), red deer (Conard and Prindiville 2000; Fiore et al. 2004; Steele 2004; Valensi 2000; Valensi and Psathi 2004), caprids (Fiore et al. 2004) and gazelle (Rabinovich and Hovers 2004).

The regularity of monospecific faunal assemblages in the Middle Palaeolithic strongly invokes Neanderthals as the prime accumulator (Gaudzinski 2006), and the predominance of a single species has led to the logical assumption that at these sites, or at least very close by, Neanderthals were selectively hunting these animals (e.g. Drucker and Bocherens 2004. Fiore et al. 2004). Furthermore, where the death profiles of the animals reveal a bias towards a certain age/sex class – e.g. adult male reindeer at Salzgitter-Lebenstedt - it is further assumed that Neanderthals were deliberately targeting and selectively taking specific *individuals* within the group (e.g. Patou-Mathis 2000; Gaudzinski and Roebroeks 2000). The resulting picture is of a selective hunting strategy, involving tactical planning about the seasonal availability of certain taxa at specific points in the landscape, and regular ‘on the spot’ decision making about which

specific individuals were to be targeted, presumably in order to maximise gain rather than to minimise risk. Any major differences that do exist between modern human hunting and Neanderthal have yet to be fully ascertained, although many have speculated that *Homo sapiens*' superior 'killing-at-a-distance' weapons systems (and upper body morphology) gave them a selective edge in the evolutionary arms race (Churchill 1993; Straus 1993; Shea 2006; Rhodes and Churchill 2009; Churchill and Rhodes 2009).

Here, we are not concerned with comparing behaviours over the Middle to Upper Palaeolithic transition, a task that is rarely undertaken impartially. Instead we take a critical look at the question of *how* Neanderthals hunted, a topic often considered too speculative. Indeed, Gaudzinski-Windheuser and Kindler (2012) have lamented the loss of a holistic approach to Neanderthal subsistence strategies, resulting in the current failure of archaeozoology to provide a comprehensive picture of the social organisation of Neanderthal hunting, the consequence of which is that 'the Neanderthals' way of life remains ambiguous and bloodless' (ibid., 66). Here focus solely on the few well-studied European kill sites and adopt a multifaceted approach that views hunting as a *chaîne opératoire* involving the decisions of both the hunter and the hunted, which together help reconstruct a picture of past events as they unfolded.

Towards a *chaîne opératoire* of Middle Palaeolithic hunting

Many European Middle Palaeolithic faunal assemblages derive from caves. Although these often provide large and discrete stratified samples, which zooarchaeologists have become very adept at reading, we suggest that they are in some respects rather ill-suited to the questions they have traditionally been used to answer – i.e. hunting practices. This is because, as is well acknowledged, they are often taxonomically diverse and time-averaged palimpsests accumulated over unknown millennia, involve multiple human and non-human agents, and are taphonomically and culturally sorted. In human terms, they provide poorer evidence on procurement and much better information on the transport of anatomical elements, species availability and, in spatial terms, 'housekeeping'. They usually lie, therefore, at the distal end of a complex *chaîne opératoire* of carcass procurement, use and disposal, leaving Neanderthal decision-making in the earlier stages little more than a rather distant memory. Many, furthermore, were excavated and curated using techniques and recording procedures that preclude a precise understanding of what was originally present, let alone its behavioural significance. This can lead to a multiplicity of equifinite interpretations for the same site, as epitomised by debate surrounding the Combe Grenal rockshelter (Chase vs Mellars vs Binford,

summarised in Mellars 1996) amongst many others¹. (This, of course, is not unique to cave assemblages, as the debates surrounding Middle Pleistocene elephant hunting at Torralba and Ambrona (Binford 1987), and the various interpretations of the Late Pliocene and Lower Pleistocene clusters at Olduvai and Koobi Foora demonstrate (Binford 1985)).

Our approach is based on narrative and focuses on the proximal end of the *chaîne opératoire*, using archaeological assemblages from death- or kill-sites. These sites sample more discrete time periods than the 'usual' cave assemblages, and preserve a more even representation of the animals killed at the locale, thus providing the most reliable information on Neanderthal hunting practices and on any deliberate prey selection that may have taken place. Their other advantage is that they enable the reconstruction of the precise landscape settings in which Neanderthals hunted – providing key insights into topographical features that could have been used to gain the upper hand in disadvantaging prey - and often the season/s of the hunt . Of equal importance is the acknowledgement that the Neanderthal hunter was only one of the agents in the chase, and that their prey had very different priorities, to protect and survive. To this end, we deploy ethological information from the hunted species, drawing on their social ecology, life histories, sensory acumen, aggressiveness and flight behaviour, to help understand the size and social make-up of the groups tackled, and how the individual members might be expected to react under pressure. Where the hunted species is now extinct, we use data from a range of living representatives to explore context-relevant family level commonalities. In sum, using the faunal *chaîne taphonomique* in the light of such ethological information, we attempt to reconstruct Neanderthal hunting *as it happened during the hunt*. Only by adopting this holistic perspective and narrative structure can we really hope to understand how Neanderthals hunted, and reveal how these practices affected the patterns seen in their domestic settings.

We approach the issue through five case studies. These are formed of well-excavated, well-understood faunal assemblages that have been posited as evidence of selective hunting strategies.

BISON: Mauran, France, MIS5a.

Mauran is situated on a low (50m) terrace of the Garonne River in the foothills of the French Pyrenees. The archaeological horizon was located ~4m below ground level and comprised ~30cm of slope deposits (clayey-silts containing limestone blocks) underlain by fluvial sediments (Farizy et al 1994). The site lies on the plateau above the Garonne and Volp rivers, palaeolandscape reconstructions suggesting that the kills took place at the end of a small gully

bounded by limestone escarpments. Pollen evidence indicates that the site was used during a period of cold, dry climate, while morphometric data on horse and bison suggest correlation with MIS5a. Some 2450 artefacts and 4193 mammalian remains were recovered from an excavated area of just 25m²; based on the ground-truthed extent of remaining deposits to the south, east and west, the excavators estimate that the total spread of material may cover some 1000m² (Farizy et al. 1994). The vast majority of the lithic artefacts were manufactured from quartzite obtained from the gravels of the Garonne river ~100m to the north, with a small flint component imported from sources >15km distance. The lithics were divided into four distinct *chaînes opératoires*: the importation of hammers for knapping stone and breaking bones, the manufacture of choppers on local rocks, flake production on local rocks, and the production of notches and denticulates on both local rocks and exotic flint. There is nothing in these to suggest that most of the lithic use at the site was anything other than *expedient* and short-lived. Furthermore, handaxes, scrapers and Levallois technology are entirely absent, suggesting that Neanderthals did not arrive at the site ‘geared up’, presumably because they knew quartzite was available locally and was adequate for the production of a simple, heavy-duty butchery toolkit. The presence of conjoinable lithics suggests that the material is in primary context, although their limited number may indicate some degree of post-depositional movement. Fire is attested to by burnt bone and fragments of charcoal, suggesting that the Neanderthals may have spent a relatively long and leisurely time at the site after the kill.

The Mauran Faunal Assemblage

The Mauran faunal assemblage is dominated by 4150 bones of bison (98.97% of the faunal assemblage), representing a minimum of 137 individuals (Farizy et al. 1994). Horse, red deer and bear make up the remaining 1.03%, with a Minimum Number of Individuals (MNI) of 3, 1 and 1 respectively. Based on the density of bison remains in the excavation and the probable extent of the deposits, it has been estimated that >4000 bison were killed at the site, representing multiple hunting events over a long period of time, perhaps a millennium (ibid.), in what can be viewed as ‘repeated communal hunts’ (Gaudzinski 2006, 140).

Both sexes are represented in the assemblage, although cows and young make up 80%, and adult males only 20% (Farizy et al 1994, 177). The age profile (Figure 1) is also skewed, with individuals three years old or younger comprising ~60% of the total; according to Farizy et al. the youngest animals are under-represented so this figure may actually be an underestimate. Very few ‘old’ animals (>65% of life expectancy or ~9 years old) are present, 4.1% according to Gaudzinski (1996). Based on patterns of tooth eruption and wear patterns, which show peaks in deciduous teeth around 6 months and 18 months of age, the excavators suggest that the

killing season fell between late summer and early autumn. Overall this pattern was interpreted as representing a catastrophic mortality profile, although not necessarily a mass death event.

FIGURE 1 AROUND HERE

The poor state of surface preservation of the bones made it impossible to determine whether there were gender biases or part selection in carcass management, although identifiable cut marks and impact fractures were present. Cut marks resulting from disarticulation were observed on many of the proximal humeri, and were also noted on the atlas vertebrae, proximal radio-ulnae and proximal metacarpals (Farizy et al. 1994; Farizy and David 1992). Cutmarks were also found on the humerus shafts, suggesting filleting (Farizy and David 1992), whereas marks on the distal tibiae could relate to either disarticulation or the severing of tendons (Boyle 2000). The systematic breakage of bones for marrow extraction is also evident, particularly on the radio-ulnae and metapodials, but also been recorded on the femora, humeri and tibiae (Farizy and David 1992). Such processing was not intensive, however (Boyle 2000). Only 18% of humeri show surface modifications, whereas 63% of metatarsals and 40% of metacarpals are complete and not exploited for marrow. The bones of young individuals showed minimal anthropogenic breakage (Farizy et al. 1994), although the excavators claimed that the lack of anatomical articulation suggests that all animals were processed to some degree. Farizy and David also noted a paucity of femora and pelvises, which is difficult to explain either taphonomically or in terms of on-site breakage patterns – they may simply have been carried away by Neanderthals. The role of carnivores, or indeed slope processes, in the dispersal of the assemblage is unclear, given its poor surface preservation.

Insights from modern bison ethology

Today, the Eurasian steppe bison (*Bison priscus* [Bojanus 1827]) is extinct, although it survived into the mid Holocene in Siberia (Kirillova et al., 2013). Any reconstruction of its social and behavioural ecology must therefore be inferred from fossil evidence and through analogy with its closest living relatives, the American bison (*Bison bison* [L., 1758]) and European bison or wisent (*Bison bonasus* [L., 1758]) (cf. Guthrie 1990). Bison are diurnal, spending much of the day feeding interspersed with “loafing and ruminating” (Meagher 1986, 6). As a genus they are ecologically flexible: the American bison are primarily grazers of wooded steppe mosaics, while the wisent now occupies deciduous and mixed forest, the areas to which they were reintroduced after becoming extinct in the wild in 1919. Palaeo-environmental evidence suggests that like the American bison, *B. priscus* favoured steppic grasslands, although the structure of the neck and hump in the fossil species indicates that they held their heads higher,

like the wisent, which might indicate an adaptation to grazing taller, sparser sward (Guthrie 1990) or a degree of browsing.

All living bison are gregarious, the size and structure of herds varying according to age, sex, season, habitat and resources (Meagher 1986). Herds can be divided into mixed (or cow) herds, and bull herds (Fuller 1960). Cow herds essentially comprise females of all ages, calves, most 2-3 years old males and some older related bulls (Meagher 1986; Krasnokutsky 1996). It is noteworthy that although the male:female ratio is 1:1 at birth, it becomes skewed with age because of relatively higher male mortality. Bulls leave mixed herds on reaching sexual maturity at 5-6 years of age; older males will join during the rut, but otherwise roam individually, in pairs or in bull herds of up to ~30 individuals (Fuller 1960; Meagher 1986). The older the bull, the less likely it is to be part of a bull herd and the more likely it is to be solitary or to exist as part of a small group of old bulls and cows.

Available resources condition herd size, with the average in North American examples (woodland and open dwelling) ranging between 11-20 animals (Fuller 1960). Larger aggregations emerge from “transient amalgamations of two to many of this basic unit” (Fuller 1960, 13) during feeding or migration. Enormous aggregations such as the famous North American buffalo jumps are vanishingly rare, and by modern accounts are literally once in a lifetime events (Frison 1978). Bison herds may be sedentary or migratory (altitudinally and directionally). Maximum horizontal distances can be in the range of 250km (Meagher 1986), although most are much smaller, on the scale of tens of kilometres (Krasnokutsky 1996). Isotopic evidence derived from the 21—16,000 year old steppe bison from the Amvrosievka site complex, Ukraine, has suggested that this population was non-migratory (Julien et al. 2012), whereas the age structure of bison (*Bison antiquus*) at Rancho la Brea, California, shows discrete age clusters 12 months apart, suggesting that herds entered this area seasonally (Jefferson and Goldin, 1989). When they do travel, bison tend to move in single file, following an adult cow (McHugh 1968).

Life expectancy is about 15 years in *B. bison*, and up to 25 years in modern populations of *B. bonasus*, although the latter are humanly provisioned in winter for conservation purposes, removing the threat of starvation and increasing survival rates (Farizy et al 1994; Meagher 1986). Sexual maturity is commonly reached between 3-4 years of age. The breeding season occurs between late June and September, with most births occurring in April-May for *B. bison* (Meagher 1986) and May-June for *B. bonasus* (Heptner et al. 1989). Physical maturity for cows is around 3 years, and bulls attain near maximum size at 5-6 years old, after which they grow slowly until finally attaining maximum weight at 10-12 years (as they are entering old age in

zooarchaeological terms). The lower third molar, used to assign age in relevant archaeological examples, erupts at 2.5 years (Farizy et al 1994), when neither cows nor bulls are fully physically mature. Population structure, based on the Wood Buffalo, Henry Mountains and Yellowstone Park herds of American bison averaged:

- Calves – 19%
- Yearlings – 13%
- 2-3 Years – 15.5%
- Adult Cows – 36.5%
- Adult Bulls – 18.5%

(calculated from data provided in Meagher 1986 and based on several sources therein. Such data are difficult to generate and are usually based on an animal's size and horn characteristics as recorded during fly-bys).

Although often described as having poor vision, field reports suggest that bison can detect a moving jeep at >1 mile distant, and a mounted rider at 0.8 miles (Fuller 1960). Their sense of hearing is also acute, and bison will react to breaking branches at distances of 100-200m (ibid). Their olfactory senses, however, are most highly developed and most important in detecting danger. They can smell humans ~500m away (Fuller 1960; Kranoksky 1996) and will take flight even when the source is not visible. On sensing danger, a 'lead' animal (often an alert adult cow) will run, which prompts the whole herd to take flight, reaching speeds of up to 60km/hr (Fuller 1960; Frison 1978). Calves may act unpredictably and run in other directions, but the adults will try to adjust their path accordingly. If the threat persists the herd will keep running and there is a danger that the original alarm may turn to blind panic, at which point juveniles and young may be trampled by the rest of the herd (Frison 1978). If the herd encounters an obstacle, the lead animal/s will veer sharply, but if the weight of animals behind is too great, the whole herd may plough forward into further danger and, in the most famous cases, over cliffs (Krasnokutsky 1996). Frison (1978) has termed this the paradox of the running herd, where the herd follows the lead animal instinctively in the blind belief that it is leading them from danger, whereas the opposite may be true. Fuller (1960, 7) observed a different flight pattern in which, once out of sight of the immediate danger, the herd paused, leaving a rear-guard bull facing towards the threat. The remaining animals would form a tight protective cluster 50-100m distant. If the threat re-emerged, the rear-guard would spin round and run towards the herd, thereby signalling it to flee. At a family level, the Bovidae are also known to show group defence against predators (Estes, 1974), the best known example being the classic circle of musk oxen defending themselves against attack by wolves (Tener, 1954), Fuller, though, suggested that cow herds tended to be shy and timid towards humans and mature bulls 'stolidly

indifferent': only rarely did bison attack and then only in situations where they were cornered and frightened, or when protecting calves (Fuller 1960, 17)

Interpreting bison hunting at Mauran

The original excavators have already used the landscape and character of the bison assemblage to provide a reconstruction of Neanderthal hunting at Mauran (Farizy et al. 1994). In this account, the topography at the site - a rocky limestone barrier fronted by open vegetation and marshy ground - provided a natural trap into which Neanderthals could drive and corral bison (Farizy et al. 1994 – see **Figure 2**). The stratigraphy and differential bone preservation were taken to indicate that the site represented hundreds of separate events over several centuries with individuals and small groups taken each time, rather than a few massive North American jump-style slaughters. Farizy et al. (ibid., 180) suggested that the season of occupation was towards the end of the rut, around August, and that the site was possibly situated along an altitudinal migration route for animals coming down from the hills of the Petites Pyrenees to winter in the valley of the Garonne. However, while the age-sex composition of the assemblage was interpreted as a catastrophic death pattern, Farizy et al. did not regard this as compelling evidence of mass kills, but rather selective killing of solitary males, females-calf units that had been isolated from the group, or maybe small groups as they presented themselves. It was clear to them, though, that a prolonged period of occupation was represented, perhaps 30-60 days per year by groups of ~30, and that the lack of anatomical associations suggested that Neanderthals processed carcasses extensively, killing only what they could eat in each hunt. In a separate analysis, Gaudzinski (1996,37) argued that the dominance of prime-aged adult cows in the bison fauna, reflects a 'controlled, focussed and selective' prime-dominated hunting strategy that occurred repeatedly over a long period of time, the inference being that selective, serial killing of small numbers of individuals had taken place (see also Gaudzinski 2006, 139-40).

FIGURE 2 AROUND HERE

We certainly do not disagree with most elements of these reconstructions. It seems very likely that the season of slaughter corresponds with the altitudinal movement of bison from the montane uplands to the low-lying river valley and beyond. As 6 month and 18 month olds are well represented in the assemblage, we might see the season of death as slightly later, around September-October, but this is still after the rutting season when dominant males of mating age would have already disbanded from mixed groups and returned to a solitary or bull herd

existence. However, we depart in seeing Mauran as the indiscriminate and routine killing of many individuals from typical cow herds.

Available herd structure figures (above) reveal that there is no significant deficit in young or old individuals in the Mauran fossil assemblage, although this of course depends on where one draws the boundaries of the age categories. Nevertheless, the assemblage is not, in our view, prime-adult dominated, at least not in a social sense. Gaudzinski's figures, from Farizy et al.'s graph (Gaudzinski 1996 Table 7) give 24.6% juvenile, 73.1% adult and 4.1% old-aged individuals. The age marker for adulthood, the eruption of the third molar, occurs around 2.5 years of age, within the second age class. As Figure 1 shows, the 24.6% of juvenile individuals captures only animals in the first 10% life-phase, any animal in the other 90% of an average life expectancy seen as 'zooarchaeologically adult' and presumed to behave in adult ways. In reality a large number of these individuals would still have been socially and physically immature until at least 3-5 years of age, the third age or fourth age class, depending on their sex. In natural populations, furthermore, old bison are not only rare, but infrequently associate with other animals and do not take part in the rut (Fuller 1960). Simply put, one should not expect old-aged individuals of either sex to be highly represented in cow herds. Likewise, the 20% figure of 'adult' males can be interpreted as socially and sexually immature individuals who had not yet left the maternal herd, rather than individual males or members of bull groups. The problem again stems from a mismatch between inferred skeletal adulthood and animal behaviour. The sex profile is largely based on long bones, in particular the distal tibia and distal metacarpal. These bones fuse between the 3.3 and 4 years of age, and bulls reach near full size at 5-6, just before they leave the maternal herd. This means that bulls with a physical age of 3 to 4 will appear skeletally adult, but would remain socially and physically immature and probably still reside with the maternal herd.

Overall our reading of the data suggests that Neanderthals did not selectively target adults, but rather unselectively slaughtered from among all animals within a typical cow herd. Mauran was a predictable post-rut feeding ground, and we can therefore view hunting practices there as a *routine* behaviour for pre-Pyrenean Neanderthals, the knowledge of the locale and its hunting potential being passed on over generations. Indeed, as suggested by the original excavators, Neanderthals repeatedly used the natural topography of Mauran – a cul-de-sac with open vegetation and marshy ground - to disadvantage bison. Exploiting their own flight behaviour to engineer a stampede, cow herds were driven against the limestone rocks, where they became a frightened mass of bison flesh, individuals concerned only with their own escape. At this point, the panicked animals were just as likely to inflict injury on their own young as were the

Neanderthal hunters, who nevertheless set about killing any animals that came into close range using hand-held spears or lances. Under such fraught conditions, it seems to us extremely unlikely that Neanderthals could make the decisions required for the selective slaughter of individuals of a specific age and sex. Instead we see this more akin to a killing frenzy - a case of 'shoot first and ask questions later'. The fact that the subsequent carcass processing at Mautan is incomplete (Boyle 2000) is further testament to the random nature of the slaughter, suggesting that Neanderthals took only what they wanted, i.e. the delicacies (fat, viscera, the tongue, and other choice fillets) from the fattest animals. The rest was left to carnivores and to the elements, explaining why the bones are largely jumbled but the lithics refit. The use of locally available lithics also shows that this can be seen as a planned practice in a well known landscape (Gaudzinski 1996, 37) as evidenced elsewhere (White 2012), a characteristic element of which was the knowledge that quartzite adequate for the production of the necessary butchery toolkit was present at the locale, as well as the knowledge of the behavioural patterns of the intended prey. The unpredictable aspect of the operation would have been the precise identity of the individuals that would be killed. These behaviours may have been repeated several times during a season without large social gatherings, and while our (possibly anachronistic) modern eyes may see this as a rather wasteful killing pattern in terms of meat consumption, other resources such as hides, sinews and brains for tanning may have been equally important as winter closed in. Whether Neanderthals preserved food is entirely moot.

AUROCHS: La Borde, France, MIS5

La Borde is situated on the eastern margin of the Aquitaine basin, the nearest watercourse being the Célé river (a tributary of the Lot) some 3km to the south (Jaubert et al. 1990). The site takes the form of a karstic depression in the Jurassic limestone plateau (i.e. an aven or collapsed cavern) located at the base of a low hill that gently rises 100m above the surrounding plateau (Figure 3). It was excavated under rescue conditions in 1971, after which the systematic sieving of the spoil facilitated the recovery of thousands of lithic artefacts and faunal remains. These seem to have been concentrated in a single horizon ~55cm thick towards the base of the depression. The age of the site is unclear, but on geological and environmental grounds, it appears to correlate with a temperate period, probably one of the warm substages of MIS5 (Mellars 1996). The excavators suggested that the site was in primary context, but that the colluviation that filled the depression had moved objects from their original positions of discard. The vertical distribution of objects within the find layer further indicated that the assemblage is a palimpsest, formed, like Mautan, by repeated visits to the locale by Neanderthal hunters.

FIGURE 3 AROUND HERE

The lithic assemblage from La Borde is largely made on locally available quartz pebbles (n=2708), with a small element of imported flint (n=101). Denticulates, notches and unmodified cortical flakes dominate the assemblage, alongside chopper tools made on pebbles. Handaxes, by contrast, are entirely absent. The small flint assemblage contains a high proportion of tools and includes evidence of the use of the Levallois technique. The faunal assemblage contains five species: aurochs (93.1%), wolf (2.2%), red deer (0.7%), horse (3.5%) and European steppe ass (0.5%).

The La Borde aurochs assemblage

The aurochs remains from La Borde represent a minimum of 40 individuals, although far more were no doubt originally present. The preservation of the bones is poor and some are covered in calcareous concretions. As such, no surface features are visible and it is not possible to determine cutmarks and fracture marks related to butchery or carnivore damage with any degree of confidence (Jaubert et al. 1990. Gaudzinski 1996, 22-3). The age and sex structure of the assemblage is informative, however. Tooth wear patterns suggest that majority of individuals are juveniles and subadults (61% aged ≤ 4.6 years old), with adults making up the remainder (Jaubert et al. 1990). Jaubert et al. (ibid.) classify the remains into 11 age categories based on tooth wear; other than the first category that covers the initial 6 months of life, each stage represents about a year (Table 1). According to their calculations, no animals over the age of 11 are represented in this population, which is unusual given that life expectancy in wild cattle can be as much as 18-25 years (Jaubert et al 1990) and suggests a paucity of older individuals. Jaubert et al. caution, however, that differences in diet between modern and prehistoric animals may have potentially influenced tooth wear stages, resulting in the age estimates that are therefore too young. This being the case, we might instead conservatively regard them as approximate 10% life-cycle categories. Even using this calculation, only 13% are beyond 65% life expectancy. Whatever the case, the assemblage is most certainly not prime-adult dominated (Gaudzinski 1996), but is dominated by immature individuals, notwithstanding that some of these animals may have had body weights close to those of adults.

TABLE 1 AROUND HERE

Based on their gracility, most of the adult animals appear to have been cows, with few or no bulls present. Jaubert et al. interpret this as a mass kill pattern of a natural living population, but one that specifically targeted nursery herds (similar to cow/mixed herds in bison). The site appears to have been exploited during all seasons – although with peaks centred around

February, April and November – and with fewer animals killed during late summer-early autumn.

Insights from cattle ethology

The aurochs has been extinct since the 17th century. Any estimation of its social and behavioural ecology must therefore rely on historical reports - of which there are a number (Van Vuure, 2002 and references therein) - and baseline data from extant species of wild cattle. (Table 2).

TABLE 2 AROUND HERE

Most of our information on the aurochs derives from late 16th Century Polish accounts of managed herds (Van Vuure, 2002). When unprovisioned in summer, aurochsen tended to separate into cow (or mixed) herds, bull herds, and solitary bulls. When artificially provisioned over winter, large groups comprising old and young of both sexes formed. However, left to their own devices, bulls only joined cow herds during mating, which, in the historical examples, occurred between August-September. Most calves were born in May-June. Managed aurochsen were generally unafraid of humans, and healthy adults had no natural predators in Holocene Europe, although elsewhere they were vulnerable to lions and tigers. Ecologically, aurochsen were generally grazers, preferring woodland mosaic habitats.

These data are consistent with what we know in general about the Bovini tribe. The basic social unit of all wild members of the Bovini is the mother and her calf, with cow herds comprising several of these units up to a modal value of 10-20 individuals. Bulls generally form separate bachelor herds of 2-10 animals, whereas older animals of both sexes tend to be solitary. In some species, mature adult males may associate with cow herds for some parts of the year, but generally in low numbers. Life expectancy ranges from 14-25, with females of all species becoming sexually mature at 3-4 years old. Males become sexually mature between 18 months and two years, although at this age they are neither physically nor socially mature. The rutting season in extant wild cattle is contingent on species, location and climate; as noted above, the last Holocene aurochsen calved in May-June.

Cattle have wide-angle panoramic vision and can discriminate between colours (Grandin 2000). Due to their horizontal pupils, cattle see vertical lines better than horizontal ones, which enable them to scan their surroundings while grazing. They are very sensitive to movement but may have problems focussing quickly on nearby objects, hence they 'spook' when something nearby moves suddenly (Grandin 2000, 64). Cattle have a well-developed sense of smell and can detect predators at least a mile away. They are also sensitive to high-frequency sound, but have a poor

ability to locate the source of sound, suggesting that hearing is not as important as scent and vision to their predator detection.

In studies designed to develop humane handling procedures, Grandin (1998) noted instinctive behavioural patterns for predator avoidance in both wild and domestic cattle. Cattle will initially turn to face a threat, but keep a safe distance. Van Vuure (2002), based on the historical accounts of gamekeepers who tended some of the last living aurochs herds in Jaktorów, Poland, reports that the animals were not afraid of humans and would not flee when people approached. Only when they were provoked, as through hunting, would they become dangerous. Cattle of all species tend to bunch together when threatened, a behaviour that can be exploited by a slow, stalking predator who can create anxiety among a herd and encourage individuals to leave whatever they were doing to join the rest of the group. Once assembled, a herd of cattle is easily manipulated via the twin principles of the 'point of balance' (a spatial and visual cue that causes an animal to walk away from a perceived threat) and the flight zone (the perceptual area around an animal in which it feels safe, and which once breached by a perceived threat will cause it to run away) (Grandin 1998). Grandin noted that the 'point of balance' in cattle lies at the shoulder, meaning that a handler (or predator) moving slowly just in and out of their flight zone and at the level of their shoulder will induce cattle to move forward, usually following a lead animal (Figure 4). A natural or man-made obstacle such as other hunters, a hill or natural barrier on the other side of the herd prevents the animals from deviating, and keeps the path more or less linear. The same effect can be achieved by adopting a 'windshield wiper' pattern (Figure 4). These behaviours can therefore be used to control a herd's movement, in effect forcing the cattle to 'flee at a walking pace'. If the predator fully enters the flight zone, the herd will run, again following a lead animal. In raised cattle the flight zone was ~30m (Grandin 2000).

FIGURE 4 AROUND HERE

Interpreting aurochs hunting at La Borde

Because of the structured age-sex profile of the aurochs at La Borde, Jaubert et al. (1990) rejected the idea that the site might represent a random natural death accumulation or a place to which Neanderthals transported carcasses. By contrast, they concluded that the site represents the hunting activities of Neanderthal groups who used the topography of the site to drive animals into a natural trap. Animals were hunted in this manner at La Borde almost year-round, with the exception of the calving season, and Gaudzinski (2006) has interpreted La Borde as reflecting selective and systematic exploitation of aurochs over a long time period. The age-sex structure was seen to reflect individuals who were preferentially taken from

nursery herds - i.e. females and sexually immature individuals - the implication being that Neanderthals selected animals based on their relative vulnerability and lower levels of aggression. Animals were butchered on-site using a tool kit of local quartz, augmented by a small proportion of exotic flint that Neanderthals were presumably carrying with them when they arrived in the locale. Jaubert et al. cautiously stopped short of providing a full hunting scenario.

La Borde certainly appears to be another example of Neanderthal use of topography to disadvantage prey, although we would argue additionally that they used the animals' own behavioural patterns against them in just as important a way. Largely in accord with the original interpretation, we view the age-sex structure of the assemblage as representing the wholesale slaughter of cow herds, perhaps numbering 10-20 individuals and dominated by female and young aurochsen. Given that old individuals are rare and tend to follow a solitary existence in modern wild cattle populations, their absence at La Borde is not surprising. Bull herds are also under-represented because they are numerically smaller, more aggressive and, as a result, behaviourally less predictable, all factors that mitigate against their desirability as targets. Presence and predictability are key.

Perhaps the most difficult thing to explain at La Borde is how Neanderthals managed repeatedly to drive groups of aurochs into a natural pit trap. The ancient aven lies at the bottom of an incline, and would have been more-or-less visible to herds coming from the south. Stampingeding a herd around the curve of the hill would necessitate losing control of it, and thus would potentially allow the lead animal time to swerve and guide the herd onto the plateau and away from danger. We assume that the aven was also far too large for Neanderthals to conceal with scrubby vegetation, but at the scale of the plateau overall, it represents little more than a small hole. Reliably guiding stampeding aurochsen to this specific point in the landscape, therefore, is a task that appears to us somewhat akin to playing golf with cows. Some form of drive may have been used, but even then we need to turn to the predictable flight behaviour of modern cattle herds to answer the question.

We hypothesize that Neanderthals understood and exploited the flight behaviour of wild cattle, in particular the way in which a predator keeping its distance and utilising the 'point of balance' can induce a herd to move forward - literally running away at a walking pace. In short, Neanderthals were the original cowboys. To get the animals to the aven, Neanderthals 'worried' a cow herd towards the slope, exploiting the incline (and/or other hunters positioned upslope but out of the flight zone) to discourage animals from drifting or escaping in other directions. In

this way, animals could be steered around the foot of the hill, ever closer to the trap. Neanderthals held back until the animals were directly in front of the aven, at which point they breached the flight zone and started a charge. Panicked and with nowhere else to go many of the herd would inevitably heave forwards and run straight into the hole. Once they are trapped, bovids will try to move up any available slope, growing increasingly panicked and jumping over each other in their attempts to escape (Krasnokutsky 1996). Younger, smaller animals tend to suffer disproportionately in these circumstances, although the whole group are vulnerable and the situation becomes increasingly dangerous for them all. In such a scenario of 'contained panic', close contact weapons such as thrusting spears are at their most effective; a hunter can effectively 'dig in', holding a spear anchored in the ground for defence, stability and, ultimately, killing, using the type of the stance Churchill (2014) has reconstructed based on the anatomy of the Neanderthal upper arm.

In summary, we see little evidence for selective hunting of individual aurochs by Neanderthals at La Borde, but rather indiscriminate killing of whole or major parts of cow/mixed herds, the young being highly represented because they were particularly vulnerable to injury in the melee. Once again, Neanderthals' knowledge of animal behaviour and how to exploit it was more sophisticated than their weapons of mass destruction.

RHINOCEROS: Taubach, Germany, MIS5e

The travertine quarries at Taubach, on the north-eastern side of the Ilm river valley in southeast Germany, have been a known source of mammalian remains, stone artefacts, and hearths since the 19th century (Kahlke 1977). Most finds derive from the 'knockensanden', a friable 'bone sand' near the base of the sequence, interpreted as having formed in a low energy environment, probably the shoreline of a seasonally-fluctuating lake within an internally-drained basin (Bratlund 1999, 80). On the basis of biostratigraphy (Heinrich 1984; Zeissler 1977; Maul 2002) and U-Th dates (Brunnaker et al. 1993), the entire Taubach sequence has been assigned to the Eemian Interglacial, MIS5e. The environmental signatures from the site provide a mixed picture. The mammalian fauna is dominated by thermophilous woodland species, but the molluscs are indicative of cool-steppic conditions and despite exceptionally preserved plant macro-fossils within the travertine, there is a notable absence of leaf impressions. For Bratlund (1999), this implied that the bone sand formed during an early phase of the interglacial, characterised by cold winters, warm summers and open vegetation. By contrast, Dusseldorp (2009), emphasizing regional Eemian pollen spectra, temperature estimates and inferred faunal habitat preferences, favoured a warmer and more heavily forested environment, attributing the

molluscan signature to a dispersal lag, and the absence of leaf impressions to localized vegetation patterns.

Neanderthal activity at Taubach seems to have concentrated on drier areas (or during drier seasons) around a series of freshwater pools. These were fed by carbonate rich springs originating in the Muschelkalk limestone of the Northern Ilmgraben, which according to Bratlund (1999), acted as warm springs that did not freeze in winter. Schäfer's (1993) interpretation of the distribution of lithics within the Knochensand suggests that Neanderthals made frequent, short duration visits to the locale, long enough to work stone, make fires and process animal carcasses. For much of the past 150 years, therefore, Taubach has been widely interpreted as the primary context remains of a series of Neanderthal hunting camps (Bratlund 1999 and references therein, *contra* Leney and Foley 1999).

The Taubach Faunal Assemblage

The Taubach fauna is dominated by brown bear, beaver, bison and Merck's rhinoceros, which together comprise ~90% of the excavated assemblage (Bratlund 1999). The extant material is, however, only a small fraction of the original assemblage, and is completely biased by historical collection practices. Teeth, jaws and complete bones are over-represented, making it unsuitable for analyses of part frequency or fragmentation patterns, although the fact that the main species are represented by all body elements and show a high frequency of cutmarks does make it possible to examine carcass exploitation patterns. It is only the rhinoceroses that concern us here.

Bratlund (1999) convincingly demonstrated that despite obvious collection biases, evidence of filleting and dismemberment can be detected on all rhino body parts, suggesting that Neanderthals had access to whole, fresh carcasses. Similarly the age structure of the known material - based on dentitions that (despite preferential collection) are unlikely to have been selectively collected by age group - reveals a clear bias in favour of young animals between 1-1.5 years of age (52%) (Table 3).

TABLE 3 AROUND HERE

Insights from rhinoceros ethology

The five extant species of Rhinoceros (white and black Rhinos in Africa and Sumatran, Javan and Indian/greater one-horned rhinos in Asia) exhibit a range of behaviours and social organisation, which are largely predicated on ecological drivers such as the density and distribution of

resources (Owen-Smith 1984; Hutchins et al 2006). Further variations were almost certainly manifest in the extinct species represented at Taubach. That said, a number of traits occur at Family level (i.e. they are common to all living rhinos, see Hutchins et al. 2006), which may therefore aid a general understanding of the patterns of rhino exploitation at Taubach.

Rhino populations can be divided into five classes of animals: dominant adult bulls, subordinate adult bulls, adult cows, calves and sub-adults (Hutchins et al. 2006; Owen-Smith 1994). They are by and large not social animals. Asian species are the least social, with adults generally only coming together to mate (Hutchins et al. 2006). The only truly stable relationship is between a mother and calf, although even this is temporary. Males of all species tend to be solitary, while females may form small groups with their calves and sub-adults; among the black rhinos, groups of 3-5 may form, while in white rhinos groups of six to ten have been reported. Sub-adults of all species may associate, sometimes forming large groups, the size of which may be constrained by the availability of particular resources such as salt licks or ponds. Rhinos are mainly active during the evening and early morning, resting during the middle of the day under trees or in mud wallows that aid thermoregulation, repel insects and provide protection from the sun; where deeper water is present, they may spend their time standing or lying in pools (Hutchins et al. 2006).

Rhino calves can be born at any time of year. A single calf is the norm, which will remain with its mother until the cow is again preparturient, at which point it will be expelled. The abandoned animal usually joins a sub-adult group. Inter-birth intervals in modern rhinos range between two and five years, depending on species. Calves generally keep close to their highly defensive mothers for their first 1-1.5 years, after which they may wander more widely; when separated temporarily they maintain contact through vocalisations (Hutchins et al. 2006; Bratlund 1999).

Females reach sexual maturity between 4-7 years old (Hutchins et al. 2006), though they might not at this point be socially mature. In white rhinos, for example, females first come into oestrus ~5 years old, but will remain in their sub-adult group until the birth of their first calf at ~6.5 to 7 years old (Pienaar 1994). Only on leaving their sub-adult group to form a cow-calf pairing are they behaviourally and socially fully adult. Sexual maturity in males generally occurs 2-3 years later than in females, and they are only considered socially adult once they become solitary and assume a dominant or subordinate pattern of behaviour. Dominant bulls of the White and Sumatran species defend exclusive territories, within which they tolerate the four other social categories (Hutchins et al. 2006; Owen-Smith 1994). White rhino bulls usually only

leave their territory to go to and from water, a risky business that can result in clashes and even death, especially during the dry season (Pienaar 1994). Black rhino males may be territorial or share overlapping ranges with other dominant males, usually with an exclusive core; the latter is also true of Indian and Sumatran rhinos but males of all species will defend females in oestrus (Hutchins et al. 2006). Bulls will also try to stop cows in oestrus leaving their territory. Mating is often a dangerous task for rhinos, and can result in the death of both males and females.

Rhinos exhibit a number of anti-predatory behaviours, depending on the sensory alarm triggered (Hutchins et al. 2006). They have notoriously poor vision and while they can spot a moving human as far as 60m away, they are unable to detect a motionless person even as close as 30m away. Their hearing is good, however, employing their tubular ears in a swivelling motion to pick up surround-sound (Owen-Smith 1984), yet in all species it is the sense of smell that is most keen. When detecting human presence by scent, they will often run away at great speed for several hundred metres. The degree of alarm is lessened when animals are able to locate humans acoustically or visually; if the distance between the human and rhino is ~30-40m, acoustic and visual stimuli rarely elicit a fear response (Hutchins et al. 2006).

Black rhinos have a reputation for aggression, and accounts of attacks are often based on this species (Bratlund 1999), although Javan and Indian rhinos will attack humans that get too close (Owen-Smith 1984). Rhino attacks are usually poorly directed (Nowak 1999).

Black rhino females are more aggressive than males (Berger and Cunningham 1995), but mothers with calves have a greater tendency to flee, especially if a threat is detected at a distance of >50m. Lone adult black rhinos tend not to flee from lions or hyaenas, but they do flee from humans (ibid.), although males often do not flee at all, and when they do, they have a shorter flight distance, a behaviour that results in males being killed more often than females (Berger and Cunningham 1995). White rhinos are generally regarded as a milder-tempered species (Owen-Smith 1984). When in groups, they will stand in a defensive formation with their rumps pressed together: a strategy more suited against lions and hyaenas than against humans. There are reports that different species display predictable calf-cow spatial relationships both when calm and when under threat - e.g. that seen in Indian and white rhinos, where the calf will run in front of a fleeing cow, whereas in the black rhino, they will run behind, although whether these patterns are a constant is open to doubt (Bratlund 1999, and references therein).

Interpreting rhino hunting at Taubach

Taubach is a palimpsest of many individual rhino hunting events, although the topography of the site, observable butchery patterns, and behaviour of the prey animals offer significant clues

to the hunting strategies Neanderthals practiced there. The immediate environment was a fairly open marshy area with warm, calcium-rich water running down from the limestone graben above the site. The waters formed streams and transient bodies of standing water in which carbonate deposits (travertine) accumulated. Bratlund (1999) has effectively dismissed earlier interpretations of rhino hunting structured around the use of pit traps (Soergel 1922), as there are no behavioural or ethnographical reasons to believe that such practices would preferentially trap young individuals. Similarly, the paucity of rhinoceros ribs and vertebrae, once taken as evidence that animals were transported to the site from kill sites elsewhere, has since been shown to be an artefact of modern collection practices (Dusseldorp 2009; Behm-Blanke 1960). So how did Neanderthals hunt rhino at Taubach?

The warm streams and pools at Taubach probably acted as magnet locations for rhinos, as midday wallows and as salt-licks, the latter suggestion supported by the presence of saline ostracods (cf. Bratlund 1999). Such an environment could have hosted diverse rhino groupings, from solitary males to groups of cows, calves and sub-adults. No data exist regarding the sex of the Taubach rhinos, although the age structure provides telling information. The majority of the rhinos killed at Taubach were young enough to be part of a cow-calf group, but old enough not to require constant maternal surveillance (Bratlund 1999). The mortality pattern at Taubach is very different from 'natural' annual mortality observed by Owen-Smith (1984) among white rhinos (adult males 3%; adult females 1.2%; sub-adults 3%; calves <2.5 3.5%; and calves <6months 8.3%), in which we might expect a dominance of young calves and equal proportions of adults, sub-adults and older calves.

Combining the evidence available, we suggest that Neanderthal ambush parties concealed themselves among the scrubby vegetation around the travertine pools, waiting quietly downwind of wallowing or salt-licking rhinos until a calf became separated from its mother. They then struck, exploiting the rhinos' poor eyesight and using long thrusting lances to deliver a fatal wound. Based on ethnographic parallels (see Bratlund 1999), the Neanderthal hunters may then have retreated to wait until the animal(s) expired, wary that the mother may come crashing through the brush at any second to aid her stricken calf, whose screams would have been heard throughout the Eemian forest. It is a pity that no sex data are available, as this might reveal whether the adults present were young inexperienced mothers killed trying to defend their offspring, or males who simply refused to flee their territory during unrelated episodes. Once the calf was dead and the adult finally departed, Neanderthals could descend upon the carcass, lighting fires to deter predators or other hostiles. They could then process the carcass at their leisure, separating the head from the body and removing the tongue for

immediate consumption, disarticulating the carpal-metacarpal joints (perhaps to remove the hide) and filleting the longbones (Bratlund 1999).

The social ecology of the modern rhino Family makes it is hard to escape the fact that Taubach preserves evidence of hunting of selected individual animals, perhaps the only sustainable strategy with such slow reproducing animals. But these targets were not prime in any sense, but rather individuals who while certainly large were still young and vulnerable. While similar single-kill hunting patterns might also be assumed for more gregarious animals such as reindeer, horse and bison, relevant kill sites involving these species point only to mass kills by large hunting parties. The size and temperament of rhinos (and also the other major prey species at Taubach, *Ursus arctos*) suggests that collective hunting was similarly practised, even in the taking down of solitary animals. Nevertheless, this provides another glimpse of a varied and tactical hunting strategy based on knowledge of the environment and behaviour of the prey species, all hallmarks of a sophisticated hunter.

HORSE: Zwoleń, Poland, MIS5a-MIS4?

The Palaeolithic site at Zwoleń is located on the right bank of the Zwolenka river immediately below the Zwoleń plateau, a relatively low plain dissected by the steep valleys of the main river and its tributaries (Schild et al. 2000; Schild 2006). The complex geological and geomorphological history of the site reveals that during the Late Pleistocene, Zwoleń was situated in a deep ravine-like valley. At the point where the horse carcasses were found, the valley narrowed to only tens of metres wide, with steep sides some 6m high (Schild 2006). To the north, the valley opened up where a tributary joined the main river, while the south presented a more-or-less flat floodplain (Figure 5).

FIGURE 5 AROUND HERE

Three archaeological horizons were identified at the site. The Lower Cultural Level was contained within an early Vistulian gravel (= Weichselian, probably MIS5a), although faunal and lithic material was often encased in blocks of floodplain silts, suggesting original discard and burial on a floodplain with later reworking *en masse* into the channel gravels. The Middle and Upper Cultural Levels were within laminated silts and sands infilling channels in the early Vistulian gravels, probably representing oxbow lakes. They have been assigned to early MIS4, before the onset of severely cold conditions (Schild et al. 2000, 190). The stone tools from these horizons are in mint condition and thus in primary context; the bones are chemically weathered, indicating exposure prior to burial.

The lithic assemblages from Zwolen are dominated by bifacial tools and manufacturing debitage that have been assigned to a Micoquian type industry. The assemblages are numerically small but nonetheless informative, indicating that Neanderthals organised themselves in the landscape in a manner reminiscent of the Mousterian of Acheulean Tradition makers from Lynford, England and Assen, The Netherlands. The lithic signatures described at Lynford and Assen have been interpreted as representing long-term planning, and curation of a lithic tool kit in advance of strategically-organised hunts, followed by tool rejuvenation in the context of use (White 2012; Schreve 2012; Niekus et al. 2011). Similar arguments were advanced for Zwolen, although more tools were made on the spot than at the other sites mentioned, possibly indicating that Neanderthals stockpiled flint there over the summer for use during winter horse hunts (Schild 2006, 230). Other species were apparently hunted in the locale at other times of the year.

The Zwolen Faunal Assemblage

Over 1000 bones and bone fragments were recovered from Zwolen, of which 408 could be identified to species. Over 60% of these were of horse, with an MNI of 38. Bison (MNI = 6), mammoth (MNI = 4), rhinoceros (MNI = 4) and reindeer (MNI = 3) are also present (Gaultier in Schild 2006). The age-sex structure of the horses is shown in [Figure 6](#). It contains a high proportion of animals younger than 2 years old, fewer animals between 2 and 6 years of age, and a dominance of mares of reproductive age. Three males are present, a three year old and two adult stallions. Overall, this profile is characteristic of a catastrophic death pattern in harem herds (Gaultier in Schild et al. 2000 & Schild 2006, 98). The younger horses fall into discrete age groups, suggesting an interval of one year between death events; one may be an unborn foetus, which would suggest the presence of pregnant mares. Gaultier (in Schild 2006) was unable to use teeth to determine a season of death, but cementum annuli analyses by Burke (in Schild 2006) suggested that most of the horses died in winter, when the animals would not have been in the best of condition; only one individual possibly represents a spring death.

[FIGURE 6 AROUND HERE](#)

The poor condition of the bones precluded detailed study of dismemberment and butchery practices; only two cutmarks were identified, both on the mandible of a juvenile rhino (Bratlund in Schild et al. 2000). However, skeletal-part representation indicated that complete carcasses were originally present, meaning that large numbers of horses died on the spot (Gaultier in Schild et al. 2000), while human interference with their carcasses is indicated by the relative paucity of meaty proximal limbs which Neanderthals presumably carried away, leaving only the

head and distal limbs behind (Gaultier in Schild 2006). Gaultier further estimated that the of preserved bones equate to less than 1% of the original assemblage, suggesting that several thousand horses might have been killed at Zwoleń. As elsewhere, the absence of intensive bone breakage and the presence of articulating cranio-mandibular sets lacking any evidence for removal of the tongue or brains suggest that processing was not intensive.

Insights from Horse ethology

Research on feral and free-ranging wild horses has shown that, like most of the gregarious species discussed here, horse society is essentially matriarchal and anchored around enduring relationships between mares and their offspring (Goodwin 1999). Classic studies of feral horses in North America (e.g. Berger 1977) established three basic social groupings:

1. The harem, consisting of a stallion, his mares, juveniles of both sexes and foals. In the herds studied by Berger, band size was 3-6 individuals. Much larger groups were reported among Venezuelan feral horses by Pacheco and Herrera (1997), with a monthly mean aggregation of 15-20 individuals and occasional groupings of ~35. Multiple stallion bands were also recorded. In these, the number of adult males present was dependent on group size: in groups of less than 20 animals a single male was the norm; in groups larger than 21 animals two or more stallions were present (*ibid.*).
2. All-male bachelor herds, generally consisting of 2-3 animals, with occasional groups numbering around 8.
3. Solitary males.

In temperate zones, horses mate and give birth during the spring (Pacheco and Herrera 1997 and references therein). Young horses remain with their natal groups until they reach sexual maturity. Juvenile males leave (or are expelled from) natal groups around two years of age, joining bachelor groups for 5 years or so before acquiring their own harem (Goodwin 1999; Gaultier in Schild 2006). Juvenile females leave the natal group between 1.5 and 2.5 years old, joining either an existing harem or a new harem formed by a promising young stallion; most mares of breeding age within a harem *will* breed (Goodwin 1999; Gaultier in Schild 2006). Harem groups tend to inhabit restricted home ranges near reliable sources of water and food, only rarely migrating outside their territory (Berger, 1986). Home ranges vary according to terrain and seasonal resource availability. Berger (1977) reported home ranges of ~48 km² in winter/early spring, down to just 8km² in summer.

Berger (1977) recorded both random and non-random anti-predatory responses among horses, depending on the immediacy of the threat and the local topography. In harem groups, random

flights occurred when danger was immediate, such as when a group of horses was surprised by a human hunter. These flights were leaderless and animals frequently fled in any direction. This type of 'every horse for themselves' behaviour is also the typical pattern among bachelor herds, regardless of the danger (Olsen 2001). Non-random flight in harem groups occurs when danger is not immediate. If the terrain is generally flat, horses tended to follow one another in single file. The most nervous mares usually initiate flight, leading the group and establishing a direction, but different individuals assume leadership as the escape progresses. Pacheco and Herrera (1997) observed that in single stallion bands, the male initially took up a rearguard position, 'pushing' the band forward, but subsequently moved to the front to lead it. When more than one male was present, the dominant stallion assumed the leadership, whereas the other males remained at the back, which Pacheco and Herrera suggested helped to maintain cohesion during flight. Goodwin (1999) also noted that, contrary to the popular image of the stallion, they were often neither the dominant nor the most aggressive of the animals in their herd, behavioural traits that may therefore have been brought out by modern husbandry practices.

Horse Hunting at Zwoln

The excavators suggested that Neanderthals chased harem groups down from the relatively snowless plateau into the snow-bound valley, where they were trapped and slaughtered at the narrowing, perhaps with the aid of structures (corrals). Other possibilities mooted included the exploitation of animals crossing a fording point (Gautier 1989) or the driving horses into the water (Schild and Sulgostowska 1988).

As with the examples discussed above, we prefer a somewhat different interpretation of the evidence, which is directed by the number, sex, age and location of the fossil remains. If we ignore the excavators' assumption that the valley was choked with snow for the entire winter while the plateau was driven clean by the wind, then there is no compelling reason for the animals to have been located on the plateau at the inception of each hunting event, or that the resources there would have been more easily accessible. The floor of the valley could instead have provided relatively lush grazing, water and shelter. Furthermore, the steepness and height of the valley sides around the site would not have been particularly conducive to steering horses down into the valley; they might just as easily have fled in another direction across the plateau, an area surely expansive enough to have allowed horses fleeing in a line to slip through any Neanderthal cordon, whether humanly-created or artificial. In fact, however one looks at it, driving the horses from the plateau into the valley seems an unlikely course of action. Jumping horses over the steep cliffs might have been an option, but it has long been recognised that the

flight patterns of horse are incompatible with such a method (Olsen 1995; Schild 2006). A simpler hypothesis that takes into account horse behaviour, the archaeological evidence and requires fewer assumptions is available.

The age-sex profile does indeed indicate that harem groups were the focus of Neanderthal hunting. Such groups were relatively easy pickings because their movements were tethered by local resources (food and water) and their structured flight behaviour rendered them somewhat more predictable than bachelor herds, making them easier - and less aggressive - targets (Levine 1983; Niven 2007). Our narrative sees a Neanderthal hunting party divided into two groups, which acted in union while serving different purposes. One group tracked harem groups on the narrow grassy floodplain, in places constricted to bottlenecks by the river on one side and the cliffs on the other. The low vegetation meant that the pursuers would remain visible to the horses and as such would not have constituted a direct or sudden threat. The other group lay in wait further down the valley, out of sight around the bottleneck. Advancing from a position that faced the bottleneck, the pursuing group violated the horses' flight zone, setting them running in their familiar and predictable straight-line pattern. As the horses rounded the bottleneck, the second ambush-party struck, a clear and present danger that caused the animals to scatter in all directions. Some horses attempted to scale the steep valley walls; others ran into the river, others continued to run out of the bottleneck or turned in the opposite direction. In the chaos, Neanderthals killed indiscriminately at close quarters; confused horses trampled other horses. Later, and at their leisure, the hunters selected which animals to butcher, and took from these only what they wanted. The remainder may have been simply left to freeze and ultimately rot on the valley floor. Once again, Neanderthals were exemplary tacticians but largely unselective executioners.

REINDEER: Salzgitter Lebenstedt, Germany, MIS3

The Middle Palaeolithic site at Salzgitter Lebenstedt is located on the northern bank of the river Krähenriedbach, a small right bank tributary of the Fuhse (see Figure 7). Some 370m² were excavated over two field campaigns in 1952 and 1977, yielding a large lithic assemblage (including handaxes, scrapers and Levallois material), rich faunal collections, palaeobotanical remains and bone tools (Tode 1953; Grote and Preul 1978; Gaudzinski 1999). The archaeology was recovered from a unit of waterlogged fluvial sediments up to 2m thick, comprising sands indicative of moderately fast flowing water, and peaty muds deposited in stagnant bodies of standing water. Much of the material derives from two units of peaty mud, although refitting bones and flint artefacts reveal vertical displacement over as much as 1m (straddling the upper and lower peat units) and horizontal movement of up to 9m (Gaudzinski and Roebroeks 2000

and references therein). Palaeoenvironmental reconstructions revealed a landscape dominated by shrub tundra, with many cold-adapted but sun-loving species such as dwarf birch and dwarf willow. The location of the kill-site is at the junction between the wide flat valley of the main river and the narrow, gorge-like valley of its tributary. The dating of the site has been much debated, although the current consensus would place it at the beginning of MIS3, about 58-54 ka BP (ibid.).

FIGURE 7 AROUND HERE

The Salzgitter Lebenstedt Faunal Assemblage

Several thousand bones and bone fragments were recovered from the two excavations, the most important published work concentrating on those from the 1952 excavation (Gaudzinski 1996, 2006; Gaudzinski and Roebroeks 2000). The assemblage is dominated by reindeer (MNI = 86), with smaller numbers of mammoth (MNI=17), horse (MNI = 8), bison (MNI =3), human (MNI=2), woolly rhinoceros (MNI = 1) and wolf (MNI = 1) (Gaudzinski and Roebroeks 2000). The reindeer assemblage is in primary context, with skeletal –part representation influenced only by bone-density related attrition. The other animals, however, reflect a fluvially-sorted palimpsest. The age structure of the assemblage is shown in **Figure 8** (ibid.). It reveals a dominance of adult individuals 8-9 years old (~33%), and a ‘stable’ presence of younger individuals. Few old individuals (>10 years of age) are present. Measurements on antler bases suggest that adult males predominate, although this size difference was not strongly evidenced in the postcranial material and could conceivably result from preferential survival. The presence of young individuals aged between 3-6 months old suggests that they died between August-October, which is in agreement with the antler data. The reindeer assemblage also showed abundant cut marks and fracture marks, indicating regular butchery and marrow extraction centred on adult individuals. Skeletal elements with a poor marrow content seem to have been largely ignored, as were sub-adult animals. The faunal assemblage has been interpreted as reflecting the slaughter of a large number of reindeer at one time, but with subsequent processing focussed on the prime anatomical parts of better quality animals (Gaudzinski and Roebroeks 2000; Gaudzinski 2006, 141)

FIGURE 8 AROUND HERE

Insights from Reindeer Ethology

Modern and Pleistocene reindeer and caribou (hereafter reindeer) belong to a single species - *Rangifer tarandus* (Nowak 1990). Several sub-species are recognised, although the most important contrast is an ecological one between tundra reindeer and woodland reindeer (Burch

1972). This division also involves a number of morphological, social and behavioural implications, but only two points of difference concern us here. First, woodland reindeer tend to be physically heavier, live in smaller groups and undertake relatively restricted seasonal migrations (perhaps just altitudinally) compared to their tundra counterparts (Burch 1972; Gordon 1990). Secondly, ethnographic observations of the woodland sub-species indicate that they are more likely to be hunted all year round, on an encounter basis, although they experience elevated predation and occasional mass kills during migration to their calving grounds. In contrast, the migratory tundra reindeer are killed mostly *en masse* during their seasonal migrations, with some supplementary encounter hunting practiced in their winter range and on small herd fragments (Kenyon 1997). We assume that on the Late Pleistocene steppe of the North European Plain, tundra reindeer are the most appropriate analogue, and consequently, we infer that the reindeer of concern organised themselves into large aggregations and undertook extensive seasonal migrations.

In modern herds, rutting takes place over 2-3 weeks in October, with most young born in late-May to early June (Gordon 1990). Reindeer calves are born precocious; they can walk after an hour, and outrun a human after a day. Calves nurse for at least a month, and while this will often extend into the winter, most will forage independently of their mothers after just 45 days (Nowak 1990). Sexual maturity is attained between 17-41 months, and females are able to conceive from about 1.5 years. Although individual body weights differ between populations – due to resource variability - within populations, bulls and cows both reach near maximum body weight during their second winter (i.e about 1.5 years of age), after which they may be considered ‘prime’. Interestingly, while most hunters of the recent past are able to distinguish between the sexes, they cannot discern the age of animals after 1.5 years of age (Skogland 1985). In captivity, reindeer have been known to live for up to 20 years, although the maximum in the wild is ~15 years, and the average longevity just 4.5 (Nowek 1990). Studies of herds introduced to South Georgia between 1911-1925 - where they have no natural predator and suffer most from winter death and falling off cliffs - showed that males lived up to 7-8 years of age, and females up to 11-12 (Leader-Williams 1980). This clearly introduces a sex bias into their populations.

According to Burch (1972), sedentary reindeer do not exist and all groups display some degree of mobility. Two well-known seasonal movements occur: to calving grounds in spring/early summer, and to wintering grounds during the autumn. The routes that the reindeer take vary according to the distribution and density of animals at the start of the move. Whether they take a repeated route or not is largely down to chance: migration routes may be stable for years, but

then change suddenly and dramatically between one year and the next, with massive consequences for the predictive abilities of their hunters (Burch 1972). When migrating, reindeer move an average of 25-30km per day, although distances of over 65km have been reported.

These seasonal patterns also affect the size and structure of reindeer herds. Aggregations occur during both migrations, although the largest concentrations tend to form in late June/early July immediately after calving. At other times, animals are dispersed throughout the landscape, but tundra reindeer may also congregate in smaller groups during winter, in and around the tree line. Sex structure within herds also varies during the year, in what appears to be a three-fold pattern (Nowak 1990). Both sexes come together for the spring migration, but females separate from the males to give birth. Immediately after calving, the sexes tend to aggregate again before once again separating for the summer. Herds re-aggregate for the autumn migration (and the rut), finally dispersing for the winter (Figure 9a). At all stages, the smaller, dispersed groups tend to be comprised of a single sex. Miller (1975, cited in Spiess 1979) identified seven permutations of band structure within reindeer: bull bands, cow bands, juvenile bands, sub-adult bands, cow-juvenile-bull bands and bull-cow-juvenile bands; Skoog (1989), by contrast, simplified this to just two: bull bands and mixed bands of varying age-sex structure.

FIGURE 9a & b AROUND HERE

The physical condition of the sexes, and thus the quality of their meat, varies annually (Figure 9b). Bulls acquire more fat than cows, which can constitute >20% of their body weight when in prime condition during the early autumn, although most of this is subsequently lost during the October rut. Cows understandably reach their maximum weight just before calving, but are also in peak condition during the autumn, just before the migration (ibid.). Reindeer are also the only extant genus of deer in which both sexes bear antlers. Males shed their antlers after the rut, pregnant females after parturition in June and non-pregnant females in March/April, and as male antlers tend to be larger than female ones, they provide a guide to seasonality. Seasonal variation also has a major effect on the structure of a reindeer's coat. Winter hair is long and brittle, and ethnographically was preferred for making blankets and sleeping bags rather than clothes (Burch 1972). As winter passes, warble fly larvae begin to hatch from eggs laid under the reindeers' skin the previous summer and proceed to eat holes in their hides. From February onwards, reindeer skins are thus considered to be almost worthless (ibid.). The best skins – those used to make clothing – are obtained during late summer, when the hair is new and the hide is repaired.

Reindeer are often regarded as easy to kill as they are normally encountered in groups, move in predictable ways and are more unwary and curious than dangerous. They are poor at detecting danger, relying mostly on smell and only secondarily on vision and hearing, and they produce a characteristic clicking noise from the knee when walking, thus announcing their presence (e.g. Burch 1972; Spiess 1979). Spiess (1979) argued that while most artiodactyls are easy to kill if hunters are familiar with their behaviour, reindeer do appear to be 'more stupid' and even easier to kill than other deer. Burch noted that reindeers' curiosity can often lead them to inspect anything out of the ordinary, rather than simply avoiding it or fleeing, which can facilitate easy ambushing, especially of calves. Furthermore, while reindeer will always flee from a recognised threat, such recognition is highly context-dependent and they are poor at transferring known threats to unusual or different contexts (Spiess 1979). The latter is important when considering the attraction that modern reindeer apparently show towards the metallic ring made by striking two rocks together, with individuals seen to walk from over a kilometre away to within striking distance to inspect the source (Gordon 1990). In a Pleistocene context, when the sound of banging rocks could only signal the presence of human hunters, this behaviour would have been highly risky.

Levels of wariness also vary according to group size: reindeer are most alert when scattered into small bands, but when massed, they are practically oblivious to danger (Burch 1972). This is very different from most other herd animals, which tend to be collectively more aware. Baskin and Skogland (1997) have a somewhat different view. They noted that reindeer predominantly react to smell because all individuals in a group become aware of threats simultaneously (and possibly recognise the agent responsible), whereas visual or aural cues may be picked up by only a few individuals who may first try to identify, and therefore assess the danger, before deciding to flee. This may be why group size is important, as the larger the group (which can extend into the hundreds of thousands), the more animals may be out of olfactory range. This may, we suppose, constitute collective obliviousness.

When frightened, reindeer tend to move downwind and uphill, which probably represents an attempt to get a better position to look at and smell the danger at hand (Baskin and Skogland 1997). According to Burch, all a reindeer hunter needs to do is to sit very still (or better, occupy a concealed position), downwind and close to the reindeers' line of travel, and they will eventually walk within striking distance. Pairs or groups of hunters may also take advantage of reindeer behaviour by dividing their duties into 'distractors/attractors' and 'ambushers' (Blehr 1990). Some hunters even stalk reindeer in plain sight, making a sudden dash at the last moment to try to get within striking distance (*ibid.*). This activity is possible because reindeer

will often take no action at all until the last second or two, and even then, will dash only a few yards before stopping to look back. If the hunter persists in their pursuit, the reindeer will turn away and continue running until out of danger, but by then it may well be too late. Blehr concluded that this particular flight pattern is designed to deal with the reindeer's main evolutionary predator, the wolf. Wolves stop stalking when they see that their prey has sensed their presence, and apparently depend on the stimulus of a running animal before starting a pursuit. This gives the reindeer the initiative, since the wolf will not pounce until the reindeer flees, while the reindeer does not want to flee unnecessarily and can, in any case, outrun a wolf over short distances. That said, some modern populations, especially those who have become accustomed to hunters armed with guns, will flee from much greater distances.

Once a herd begins to run, individuals may clump together. While it is not easy to predict the path of flight, reindeer are easily guided into traps, either using the natural topography or man-made corrals or drivelines, all of which serve to cut off alternative escape routes. This is traditionally done using human beaters, cairns (the Inuit traditionally use *inukshuit* - human-shaped cairns) and sticks hung with fluttering attachments, sometimes accompanied by simulated wolf howls (Blehr 1990). Reindeer also tend to course along a feature such as a river before attempting to cross it, even if it may be easily crossed when first encountered, and this is often used to the hunters' advantage (Spiess 1979). Given that modern hunted populations recognise the human figure and smell as a threat, this makes driving them easier. Collective drives are generally unselective; hunters take whichever individuals run into the trap. Depending on season, however, some form of age-sex bias is likely (Spiess 1979). In north east Alaska, spring hunts (post-calving) tended to take single age-sex bands and cow-juvenile bands, autumn hunts cow-juvenile-bull herds, alongside some bull herds that remain separate before the rut. Winter hunting would take a limited number of whatever age-sex group was most common in the area, which would largely depend on the environment, given that males are able to tolerate harsher conditions (Spiess 1979).

Reindeer Hunting at Salzgitter Lebenstedt

Gaudzinski and Roebroeks (2000) interpreted Salzgitter Lebenstedt] as clear evidence for autumn reindeer hunting by Neanderthals. Driving animals along the main valley, and diverting them into the mouth of the tributary, Neanderthals then slaughtered them. They were unable to decide whether Salzgitter Lebenstedt represents one or more hunting episodes, but suggested that Neanderthals killed numerous animals at once and then preferentially butchered adult male individuals.

The condition of reindeer at different times of the year dictates that males are usually taken before the rut and females are taken after. We may conclude from the treatment of the carcasses that the males at Salzgitter were hunted before the rut and were therefore very much in their 'prime'. We must emphasise, however, that hunters find it very difficult to determine the age of the animals they kill – although they can usually determine sex – and such age selectivity must presumably reflect either pure chance or as Gaudzinski and Roebroeks suggest, the *post-mortem* selection of the fattest animals, not a deliberate targeting of specific individuals during the hunt itself. The age structure of the reindeer hunted at Salzgitter is actually difficult to reconcile with a living population. Comparing Salzgitter with Skoog's (1968) data for a 'natural' herd structure during the autumn (Figure 10), it is very clear that adults over 6 years old are disproportionately represented in the archaeological sample, and that young animals are under-represented. This leads us to the conclusion that the archaeological assemblage is even more biased than Gaudzinski and Roebroeks recognised. Among modern populations, even those with no natural predators, males rarely live beyond 7-8 years old.

FIGURE AROUND 10 HERE

Interpreting this situation in the light of the case studies for other taxa discussed above, we naturally agree that Neanderthals intercepted a band of reindeer migrating towards their rutting ground, unselectively killing many of its constituent members. The overall age-sex structure of such groups is hard to predict, and depends on herd size and what animals were passing through just when the Neanderthals decided to attack. Perhaps the size of many of the animals in this group was a trigger. That Neanderthals later selected the fattest males for processing is uncontroversial, although whether these animals and other specimens with a decent pelt were dragged to a processing spot or processed where they fell is unclear from the records. The former might certainly help explain the age profile. Regardless, the hunt itself would have certainly required planned division of hunters into distractors and ambushers, one group using the main valley of the Fuhse as a conduit for driving migrating reindeer, collectively 'worrying' them into the mouth of the tributary. Every mobile member of the society could have participated in this task, with such docile prey even children could have acted as noisy distractors blocking the route along the main valley. As the reindeer fled up the side valley, the ambush was sprung and everything that came into the Neanderthals' path was killed. Every dead animal was skinned - the average Inuit individual required 25 reindeer skins each year and reindeer pelts are considered to be at their best during Autumn (Spiess 1979) - and the fattest individuals, who were generally the older males, were selected for extensive field butchery. The dividends from those individuals selected were carried away from the kill site for extensive processing, the rest of the carcasses left to rot.

Conclusions: shoot first, ask questions later, eat well

Our conclusions about Neanderthal hunting tactics are summarised in Table 4.

TABLE 4 AROUND HERE

As Gaudzinski (1996, 2006) has previously noted, the repeated occurrence of monospecific faunas across Europe shows that these were not regionally restricted behaviours but part of a widespread phenomenon involving ‘the interception of entire herds or aggregations of many individuals at waterholes, water streams, or along their migratory route’ (Gaudzinski-Windheuser and Kindler 2012, 61). Her comparison of the Mauran, Taubach and Salzgitter Lebenstedt assemblages suggested that Neanderthal hunting tactics, however systematic, were quite varied over time and space, adapted to prey that was either solitary or aggregated, and which ranged from young individuals in the case of megafauna, prime-aged individuals in the case of bovids and even the seasonal ‘harvesting’ of mature hibernating bears (e.g. Balverhöhle: Gaudzinski-Windheuser and Kindler 2012, 62 and references therein). This variability represents tactical flexibility that ‘could reflect very efficient [Neanderthal] adaptation to the environment, mere opportunism, or both’ (ibid).

We certainly share the view that the recurrent use of the selected sites shows that they were not singular events, and it is implausible that Neanderthals found themselves randomly presented with opportunities to kill herds of the same taxa, at the same locales, time and time again. These were, by contrast, planned encounters; the presence of prey herds was predictable, either year round (aurochs at La Borde, rhino at Taubach, perhaps horse at Zwoleń) or for brief periods during seasonal cycles (such as the end of the autumn rut for bison at Mauran or migration of reindeer at Salzgitter Lebenstedt), and that is why Neanderthals were present at these places. Neanderthals were also accomplished ethologists, aware of the behavioural foibles of different taxa and able to choose their hunting strategies accordingly. In terms of strategic and tactical flexibility, our reconstructions certainly suggest the recurrent use of driving and trapping of herds, driving and ambushing of herds, and stalking and ambushing of individual animals (at least in closed interglacial forests), all using of the natural topography and the animals’ own social and avoidance behaviour to their advantage. We depart from previous interpretations of multiple mono-specific kill sites in our suggestion that after the initial tactics were decided upon – where to go, when to go, who would go, which herds or aggregations to target, where to position distractors/beaters and ambushers, where to drive, where and when to ambush, etc. – the killing stage actually involved very little ‘selection’ or conscious decision-making. Neanderthals simply could not reliably pick out individuals of a specific sex or age –

individuals who were larger, faster, stronger and dangerously frightened - during a sequence of rapidly unfolding events that was never entirely in their control. Instead, we agree with Spiess (1979), whom 37 years ago argued that selectivity is a luxury known only to more recent hunters armed with guns or powerful bows. When pursuing large numbers of animals, the final stages in Neanderthal hunts were marked by chaos, a killing frenzy that precluded any on-the-spot targeting of individuals. It was all that Neanderthals could do to spear, indiscriminately, those unfortunate individuals who came within the effective ranges of their weapons, probably during a few terrifying minutes in which the animals were in as much danger from their conspecifics as their Neanderthal hunters.

To paraphrase Bar-Yosef's observation that Neanderthal procurement strategies can be reduced to "eat[ing] what is there" we might add that during the actual hunt their strategy can be similarly reduced to 'kill what is there...before it kills you'. It was only once the kill was complete that Neanderthals decided which carcasses to process, and which to ignore. So, Neanderthals could here reasonably be characterised as careful tacticians, casual executioners and discerning diners. In essence, then, we see no reason why Gaudzinski's interpretation of the Salzitter Lebenstedt assemblage need not apply to the others we have considered.

We are not, of course, suggesting that this was the Neanderthals' only hunting strategy. They clearly took advantage of scavenging opportunities (e.g. Stiner 1991, 1994), dispatched weak or vulnerable individuals (such as elderly or injured pachyderms, young rhino: Bratlund 1999; Gaudzinski 2004, 208; Schreve 2012), targeted non-gregarious individuals and hibernating bears, as sites such as Lehringen, Gröbern, Aridos, Taubach and Balverhöhle clearly testify. Nor are we suggesting that Neanderthal hunting always or by necessity involved the slaughter of large numbers of individuals, which is rather dependant on ethology, circumstances and luck. However, we eagerly await a convincing Middle Palaeolithic example of a targeted, isolated killing of a medium-large gregarious herbivore.

Processing at the kill site is not, however, the end of the 'chaîne taphonomique', and over 50 years of faunal studies have left a clear impression of what occurs at domestic sites, although as stated above, it seems that no two workers can readily agree on their meaning. Kill sites allow us to start at the beginning, from known carcass states and with observable selection for animals and body parts. Tacking from kill to consumption offers new potential for understanding cave assemblages. In the light of these cases studies, how are we now to interpret cave assemblages dominated by meaty adult limb bones and high fat content items, alongside the by-products of skinning such as phalanges and heads? Traditionally this would be

seen as a scavenging pattern with a few early access carcasses overprinted rather than fussy carcass processing and hide transport (the hides also serving as containers for transport). Equally, would a cave dominated by prime adults be indicative of selective targeting of solitary individuals or selective transport of these elements from mass kills? The presence of anti-social animals on the other hand must reveal a different class of hunting behaviour based around individuals, as at Taubach. Our conclusions also have implications for the interpretation of patterns of physical trauma seen in Neanderthal skeletal remains, supporting, we believe, the original conclusions of Berger and Trinkaus (1995) that injuries among Neanderthal resulted from high-risk hunting strategies that involved close encounters of the herbivore kind, rather than the later notion of interpersonal violence (Trinkaus 2012), although we suspect both were also high dopamine activities. We further suspect that a review of early Upper Palaeolithic hunting tactics might show that Aurignacian hunting was not very different from that of the Neanderthals.

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Age Class	MNI / %	%
0-0.6	1	2.7
0.6-1.6	1	2.7
1.6-2.6	5	13.9
2.6-3.6	5	13.9
3.6-4.6	10	27.8
4.6-5.6	5	13.9
5.6-6.6	4	11.1
6.6-7.6	1	2.7
7.6-8.6	3	8.3
8.6-9.6	0	
9.6-10.6	1	2.7

Table 1: MNI for aurochs age classes at Mauran (after Jaubert et al. 1990)

Species	Latin Name	Distribution	Habitat	Longevity in Wild	Sexual maturity females	sexual maturity males	Breeding	Sociality	Herd size
Banteng	<i>Bos javanicus</i>	southeast Asia	open woodland	14-17	2-4	2	Year round or seasonal depending on region. Gestation 10 months.	Form cow herds and bull herds. Cow herds usually accompanied by single adult male. Old cows and bulls tend to be solitary.	Between 2 and 40. Temporary combinations of these units into groups >100
Gaur	<i>Bos gaurus</i>	south & southeast Asia	ecologically plastic: open, wooded and disturbed areas, high and low elevation	~20	3	2	Year round or seasonal depending on region. Gestation 9 months	Fluid but generally form cow herds and bull herds. Males associate with cow herds during the rut, and occasionally at other times in varying numbers.	5-12, rarely >20
Kouprey	<i>Bos sauveli</i>	Thailand, Cambodia, Vietnam (probably extinct)	open deciduous forest in areas with extensive grassland	~20	unknown	unknown	Rut in April, births in December-February	Cow herds comprising females and their young, plus small bull herds of batchelor adult males	Cow herds usually ~20 individuals
Water buffalo	<i>Bubalus arnee</i>	south & southeast Asia	tied to water and prefer low-lying alluvial grasslands; riparian forests and woodland also suitable. Make seasonal migrations.	25	2-3	18 months	Peaks in October-November, some populations breed year round. Gestation 10-11 months.	Cow herds comprising females and their young, plus small bull herds of batchelor adult males	Cow herds usually 10-20, occasionally >100. Bull herds up to 10 individuals, older males generally solitary.
Yak	<i>Bos mutus</i>	China, India and Nepal	alpine tundra, grasslands and cold deserts, high elevation	16	3-4	2	July- September. Gestation 9 months.	Adult males often travel with females and young, although older males form bull groups and travel separately.	Basic unit 10-20 may form aggradations >100. Bull groups usually 2-5 individuals.

Table 2: Ecological, Behavioural and Social Characteristics of five Asian Wild Cattle Species (Data from Timmins et al 2008a for Banteng; Duckworth et al 2008 for Gaur; Timmins et al 2008b for Kouprey; Hedges et al 2008 for Water buffalo; Harris & Leslie 2008 for Yak).

Age Class	MNI (n=76)	%
Calves newborn	4	5.3
Calves 1-1.5 years	40	52.6
Subadults <4 years	7	9.2
Adults	25	32.9

Table 3: MNI and Age Classes of Rhinoceros from the Taubach knochensanden (after Bratlund 1999)

Taxon	Site, age	Hunting tactics: locating the prey	Hunting tactics: disadvantaging the prey	Hunting tactics: exploitation of prey behaviour	Hunting tactics: killing techniques	Hunting Strategy	Butchery practises
Bison	Mauran, MIS5a	Predictable autumn rutting and feeding grounds	Use of topography as natural trap	Exploits flight behaviour	Unselective killing of mixed herd	Driving and trapping	Selection of choicest fat, fillets and rump
Aurochs	La Borde, MIS5	Animals probably present in region all year-round	Use of topography as natural trap	Exploits flight behaviour	Unselective killing of mixed herd	Driving and trapping	Little evidence of selection
Rhino	Taubach, MIS5e	Animals predictably attracted to springs as water sources and salt licks	Use of topography for concealment and observation	Exploits inexperienced calves separated from mothers	Selective killing of calves when opportunity presents itself	Stalking and ambush	Butchery of selected individuals
Horse	Zwoleń, MIS5a or 4	Animal movements predicted by the distribution of their resources	Use of topography (bottleneck) as means of disadvantaging and ambushing	Exploitation of flight behaviour	Unselective killing of mixed herd	Driving and ambush	Selection of choicest meat
Reindeer	Salzgitter-Lebenstedt, MIS3	Predictable (i.e. known) autumn migration route	Use of topography (valley) to channel prey	Exploits avoidance behaviour, possible use of noise to 'attract' reindeer	Unselective killing of mixed herd	Driving and ambush	Selection of largest & fattest individuals

Table 4: Summary of organisation of hunting at the five sites considered.

Figure 1
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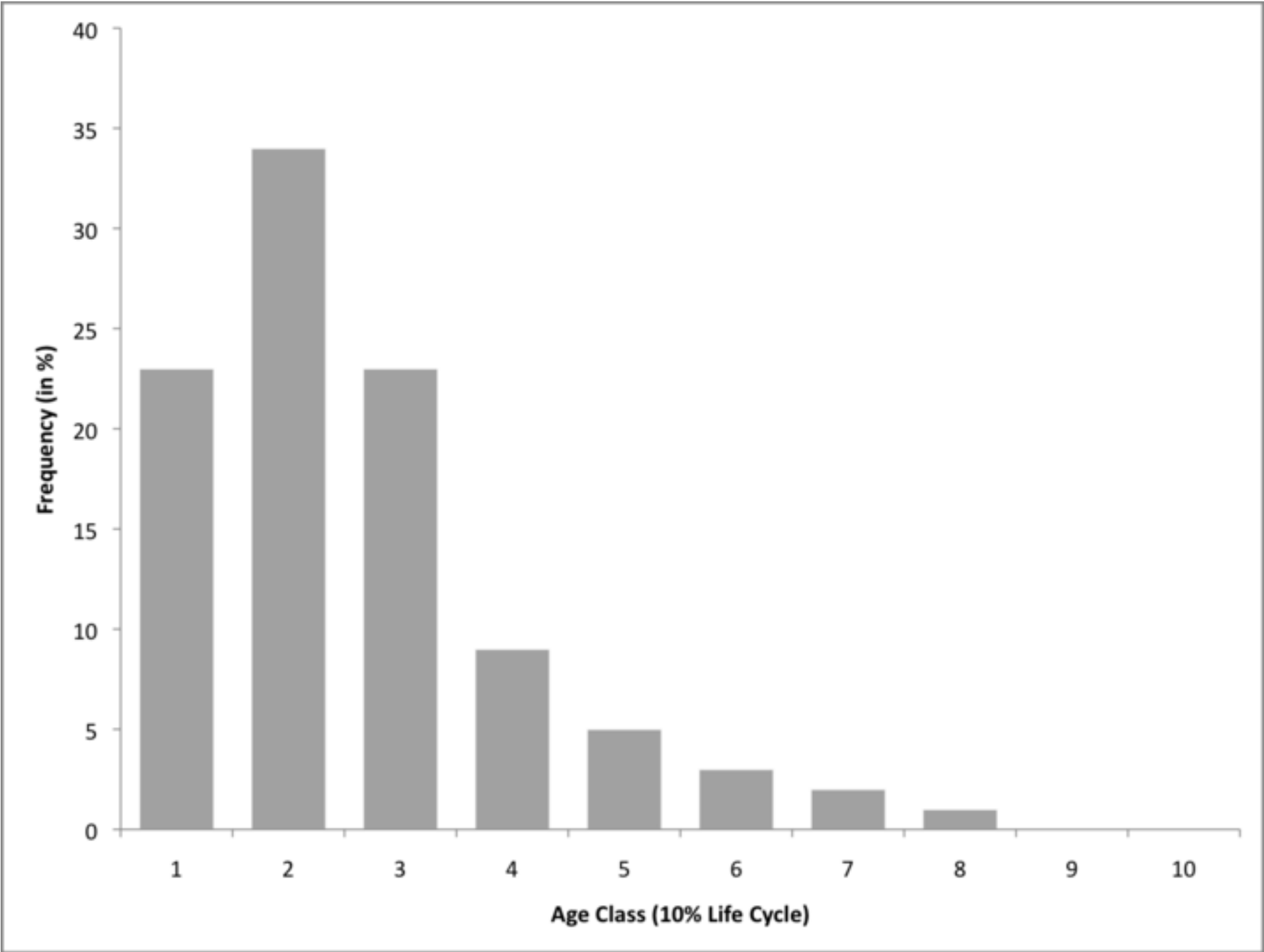


Figure 2

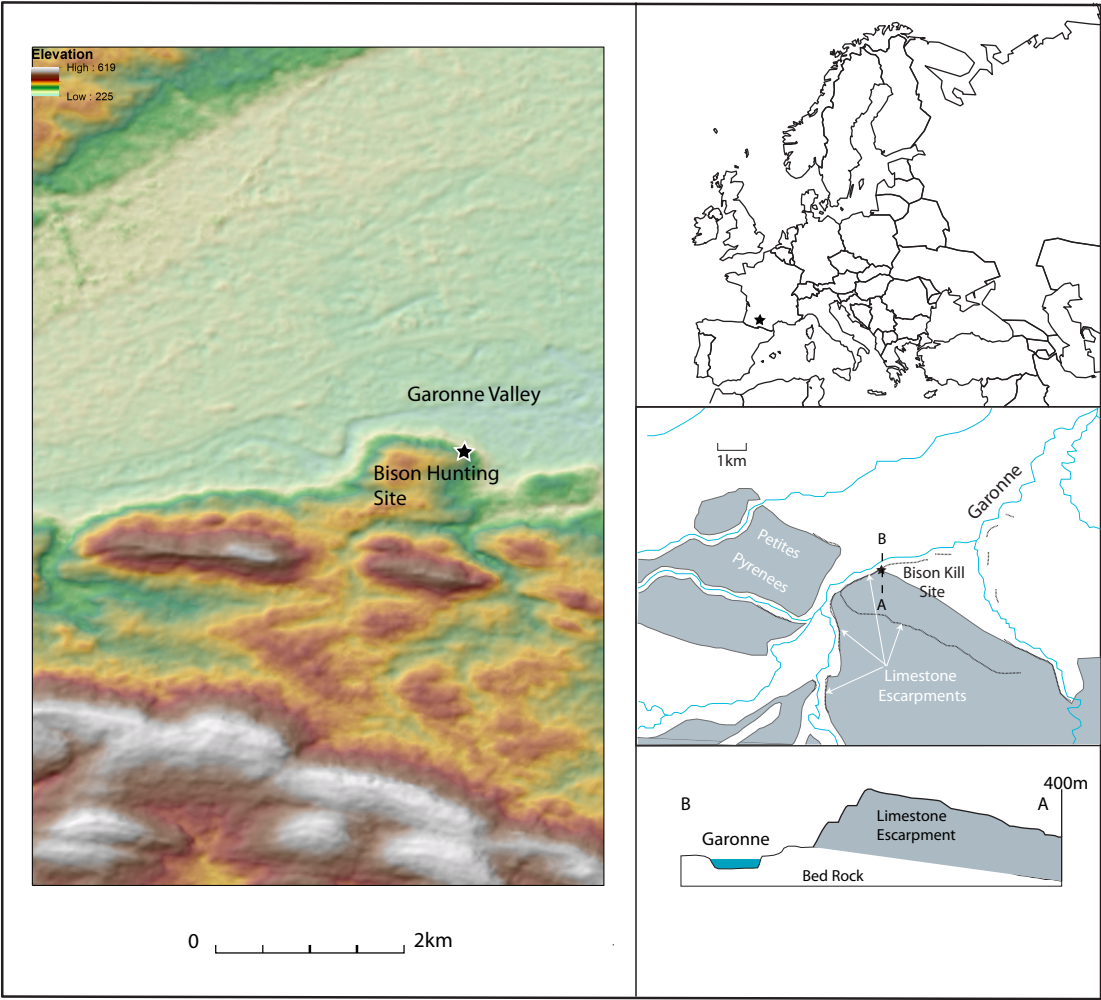


Figure 3

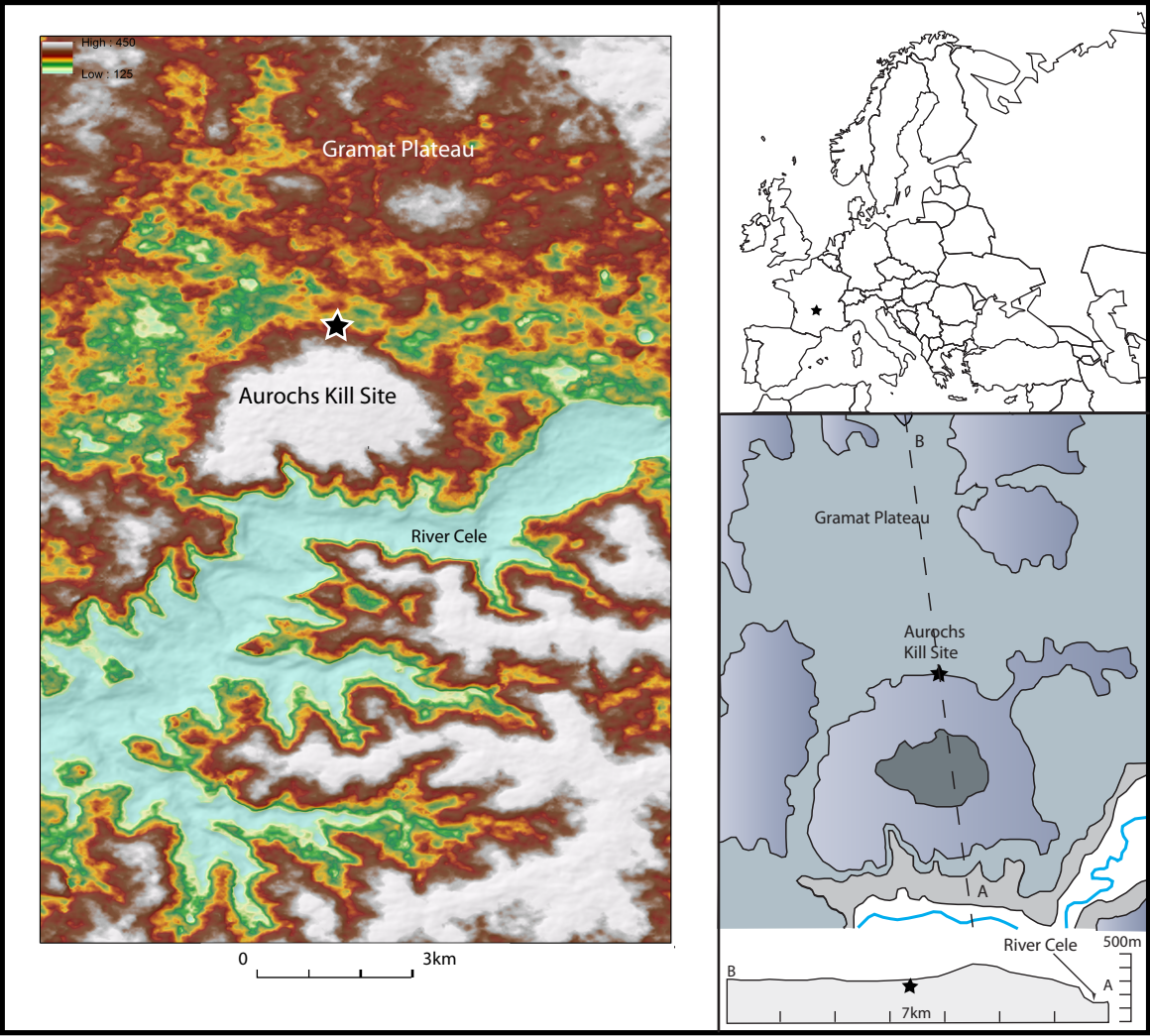


Figure 4

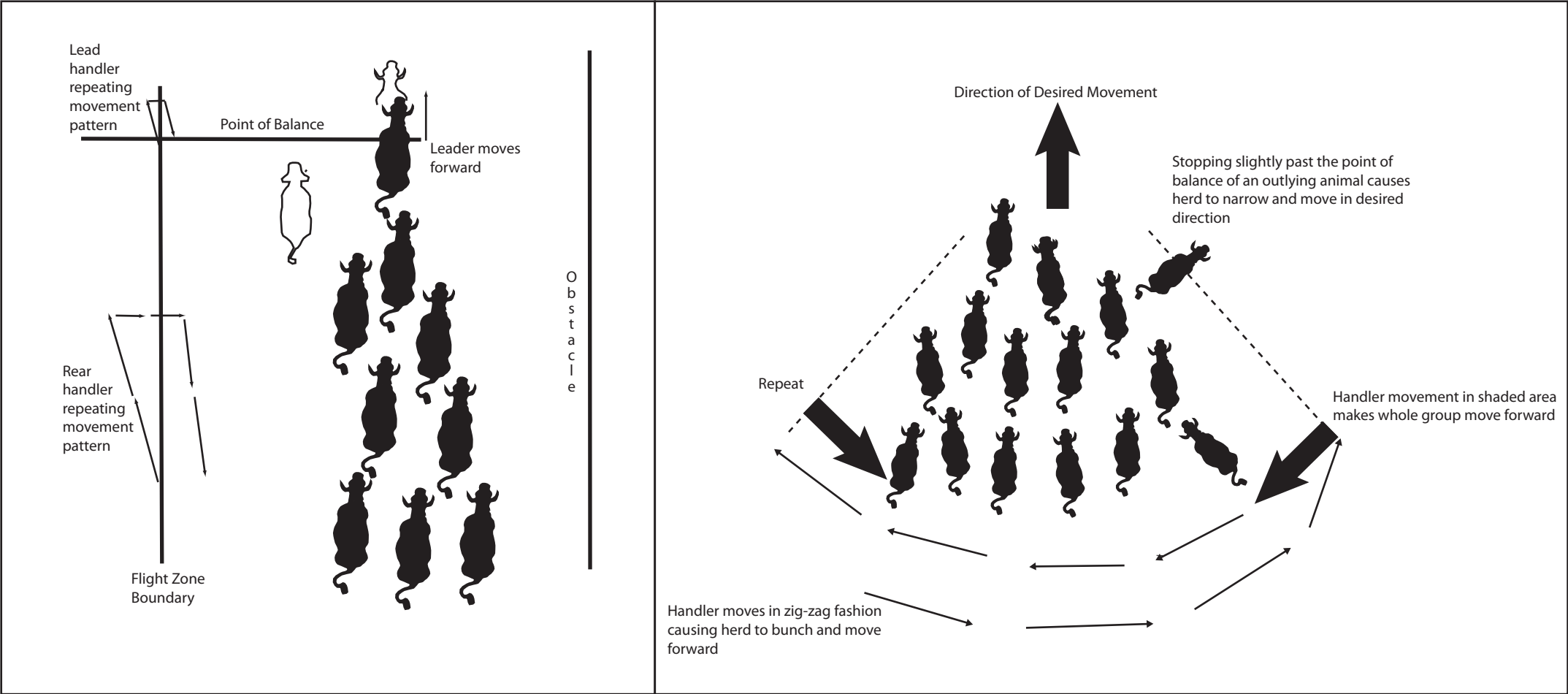


Figure 5

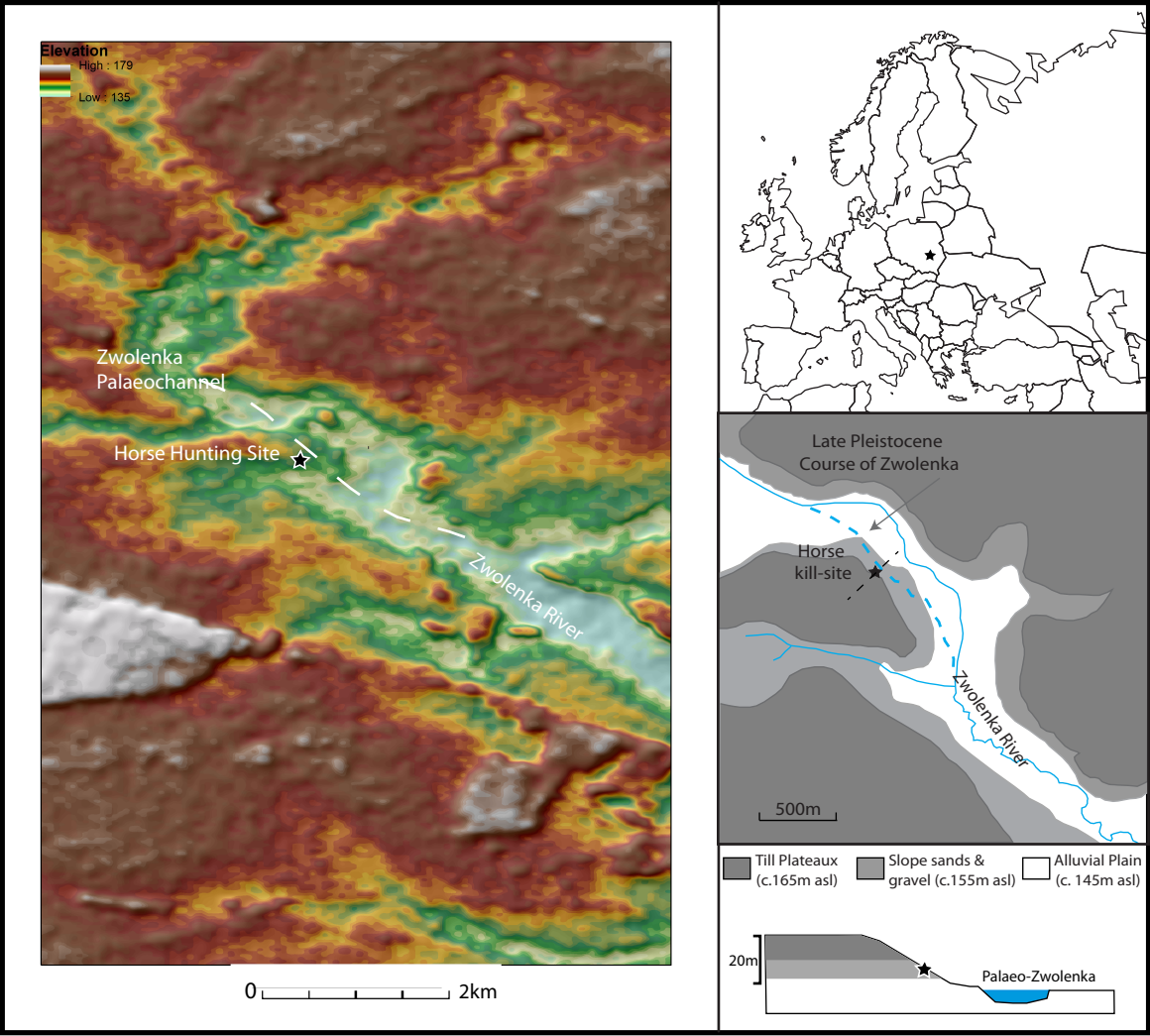


Figure 7

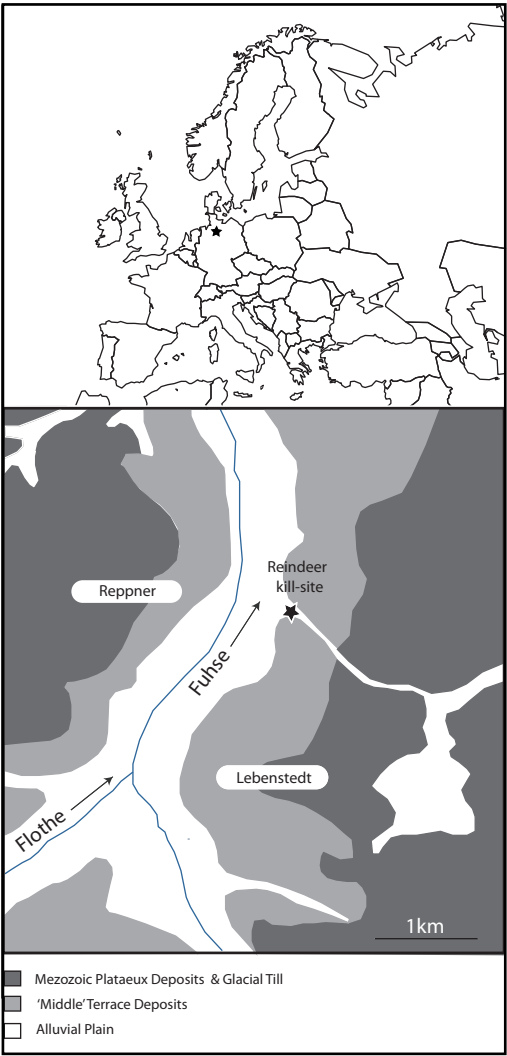


Figure 6

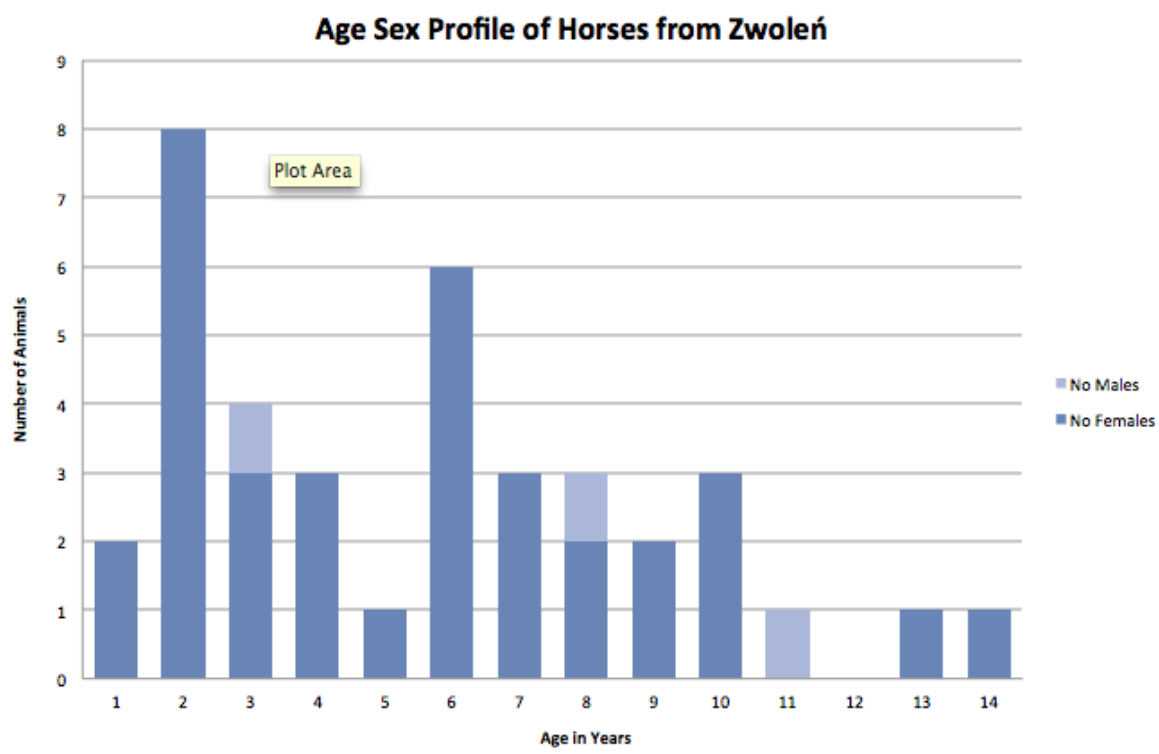


Figure 8
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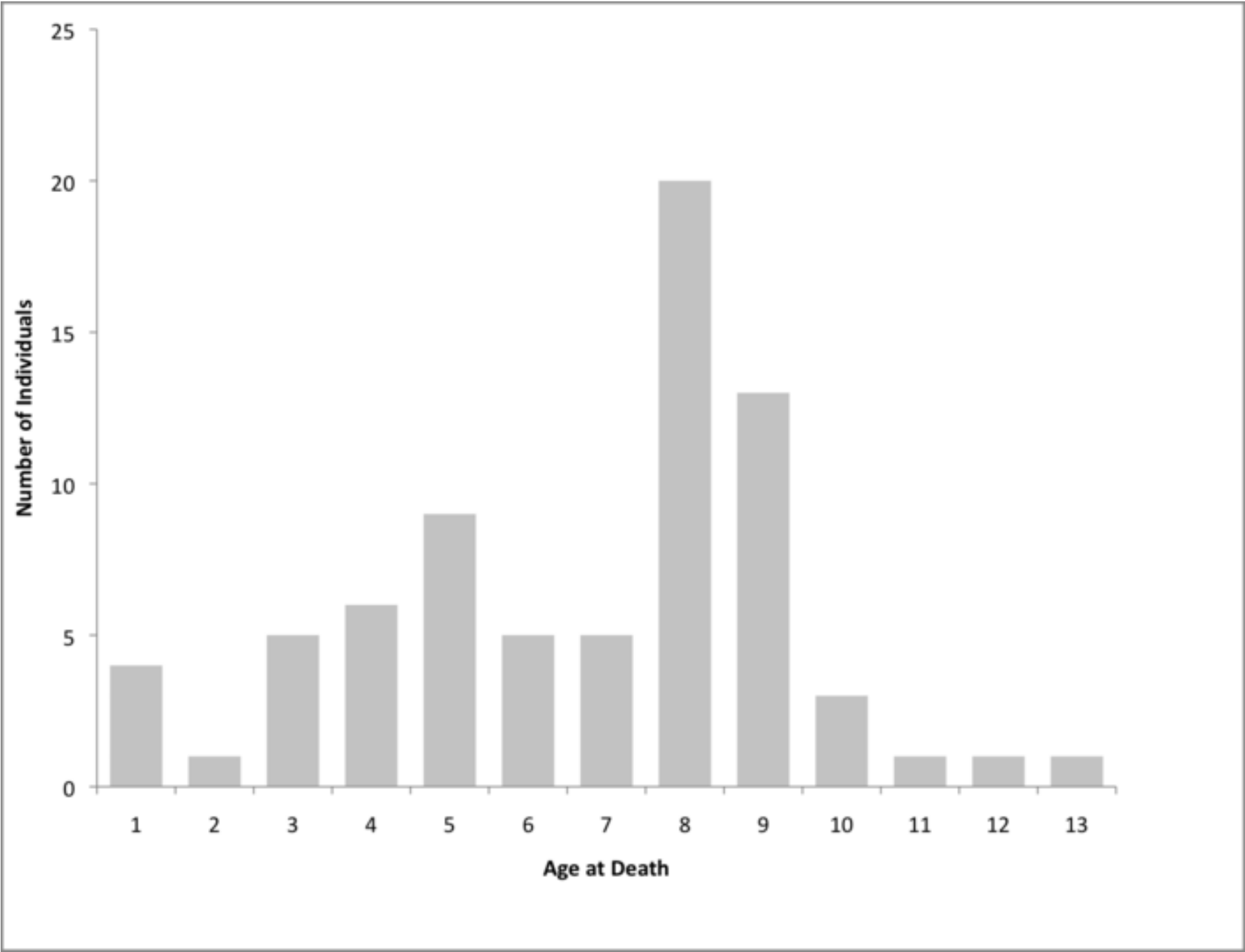


Figure 9

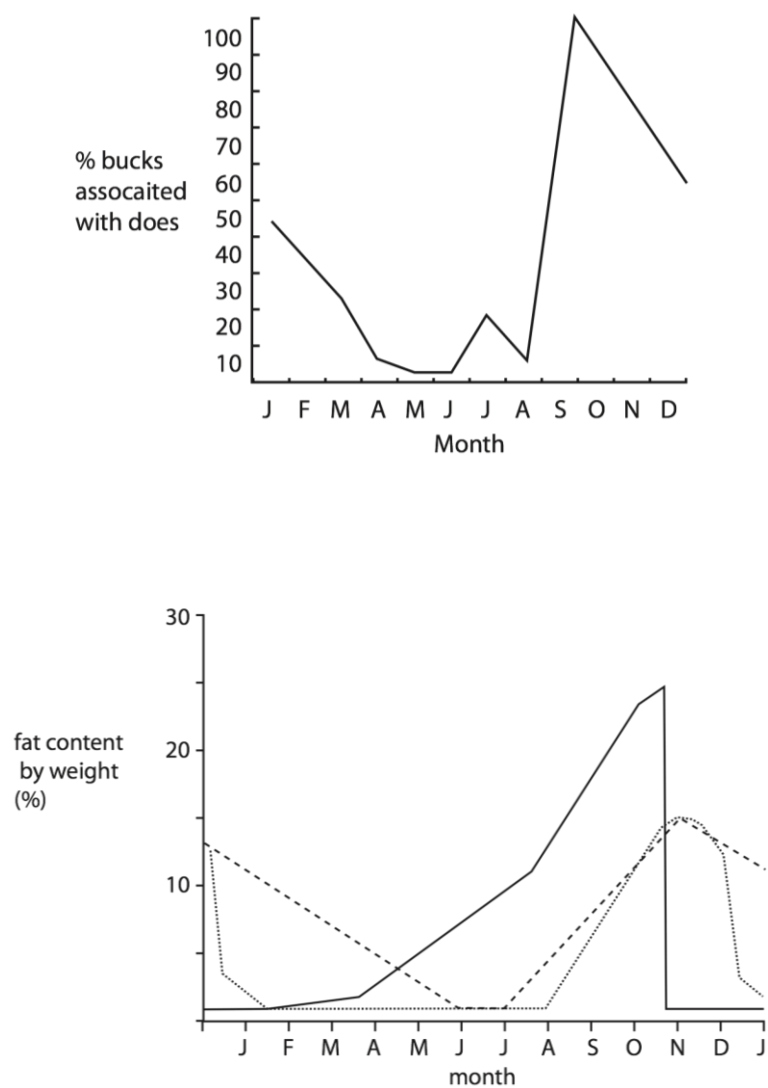
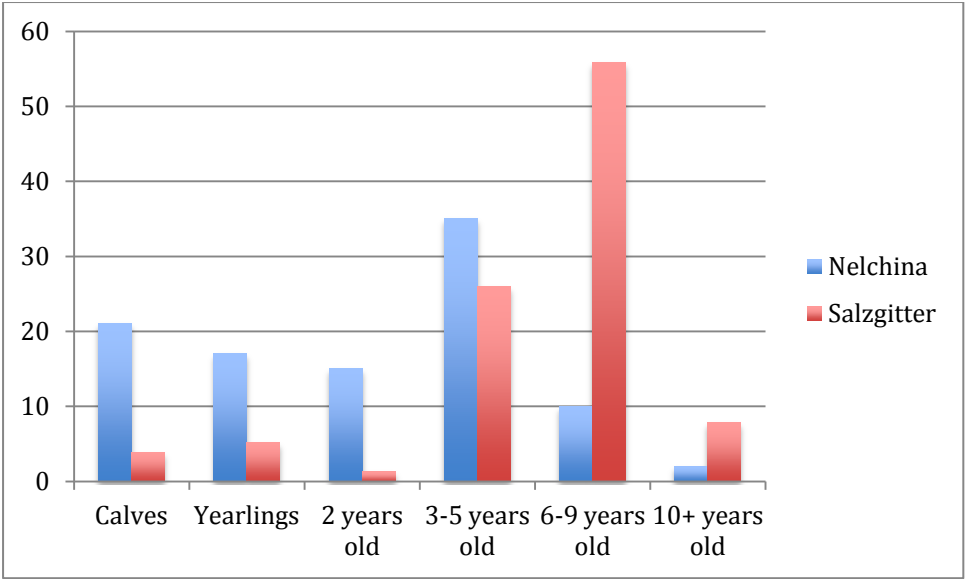


Figure 9: a) Frequency of association of bucks with does in Mainland Norwegian reindeer herds (after Skogland 1989); b) Fat Content by weight in Alaskan reindeer. Solid line – mature males; dashed line = females; dotted line = immature males

Figure 10



Highlights

- Neanderthal hunting involved superb tactical planning, using the landscape to disadvantage prey
- Their prey's avoidance and flight behaviours were also exploited in the hunt
- They did not target specific individuals during the hunt, but killed indiscriminately from cow herds
- After the kill only the 'prime' animals were chosen to butcher.
- In sum Neanderthals were careful tacticians, casual executioners and picky diners

Reviewer #1:	Response
<p>That said, the elephant in the room is Gaudzinski 2006...which... reviews the evidence from 31 bovid kill-sites, including La Borde and Maura (albeit without providing many details) and discusses Taubach and Salzgitter-Lebenstedt. The methods used by White et al. and Gaudzinski are similar and their conclusions are also very similar.</p>	<p>Complete. There is actually a strong degree of divergence between our views and those of Gaudzinski, which we have now made clearer in the MS.</p> <p>To this end, we have strengthened our use of Gaudzinski 1996, and in particular worked in (in several places including the concluding discussion) Gaudzinski 2006. We make it clear in the discussion exactly where we depart from Gaudzinski, namely in our conclusion that Neanderthals did NOT target specific individuals during the hunt. This is effectively what Gaudzinski argued for Salzgitter Lebenstedt, but she distinguished between that assemblage and all others that she considered. In contrast, we see no difference between Salzgitter and the other sites, and make this clear in the concluding discussion. We have also worked in Gaudzinski and Kindler 2012.</p>
<p>It would be good if White et al could reference Gaudzinski (2006) and discuss the implications of their interpretation of two bovid kill-sites (Maura and La Borde) for Gaudzinski's interpretation of bovid kill-sites in general. Do the authors think that the more general conclusions drawn by Gaudzinski no longer hold?</p>	<p>Complete. See comments above; also, Gaudzinski's general interpretation of bovid kill-sites is that they represent systematic, selective kills over long time periods. We have no problem with this. Our interpretations differ, however.</p> <p>We see no reason to invoke any systematic thought at the hunting stage, but rather at the stage of selecting which dead animals to process (hence out title of 'shoot first, ask questions later). We have worked in Gaudzinski 2006 in several places (Maura; La Borde,</p>

	the concluding discussion) and we make clear how we depart from her viewpoint.
Why not include Amvrosievka, for example? It is another bovid dominated killsite that could offer a fresh perspective.	<p>Amvrosievka is mentioned on page 6. However, it is a 16-21ka BP Upper Palaeolithic (Modern Human) site, and thus of no relevance to our paper on Neanderthal hunting behaviour.</p> <p>Regarding site choice in general, we have used the best and most recently published kill-sites. There are a few others, but these generally conform to the pattern and exhaustive treatment of every possible example would not add anything further</p>
Reviewer #2:	
<p>Sometimes the ethological pictures presented are somewhat generalised (and perhaps overlong) - I would like to see them related more closely to the specific topographic and vegetative situations at each of the selected case studies, rather than being provided with a list of everything the authors have found out about each species. So, for instance, analogies are drawn with modern bison / wisant, which are described as ecologically flexible, and isotope evidence is cited suggesting that bison may not always be migratory - but this is not specifically explored in the case study of Mairan, where migratory behaviour is assumed, and not demonstrated.</p>	<p>We do not agree that this statement is justified but we have nevertheless pruned out a few lines that the reviewer may have found overly detailed. On the contrary, we have selected only ethological information that is specifically relevant to aspects such as social structure, flight patterns and other behaviour of relevance, in order to gain insight into how Neanderthals potentially exploited these animals. We make clear reference to relevant topographic situations at each site and discuss any palaeobotanical information available. It is important to remember, however, that even where there is pollen or plant macrofossil evidence present, we can only use this to infer a broad picture of vegetation cover (or lack of), rather than reconstructing the position of every tree and bush on the landscape.</p>

	<p>The reference to migrations at Mauran has been replaced with text related to the post-rut period, which is what actually matters here.</p>
<p>The authors make a good job of discussing how Neanderthals could have exploited herd behaviour and landscape to kill prey, but less time exploring how local landscape and vegetation would specifically have affected prey behaviour. This could be tightened up.</p>	<p>Additional detail has been added to all case studies where available.</p>
<p>The illustrations are uniformly poor and overly schematic...perhaps use a DEM of the local setting, with an inset showing location - geology could be draped over these.</p> <p>Where given, the cross sections are mostly useful and should be included.</p>	<p>DEMS and a location map of Europe have been added to the figures. We have constructed a tripartite image which retain our original schematic plans. We feel that these assist interpretation, as the DEM data shows a modern landscape with more recent drainage patterns etc, and anthropogenic interference.</p> <p>We have enhanced the captions to explain the diagrams.</p> <p>The digital elevation data for Salzgitter, a landscape that has been glaciated since the Neanderthal occupation and is now a heavily built up area, was found to be unusable and did not aid visual interpretation.</p>
<p>Page 2, para 1 I think the authors are over-egging the pudding in their presentation of universally accepted evidence for selective hunting, and should be wary of constructing a straw man</p>	<p>This paragraph has been amended and toned down.</p>
<p>Page 13, para 1: This method of herding cattle by acting like a predator is a little confusing and difficult to understand - it could be explained more clearly (eg. in</p>	<p>The caption has been enhanced to explain the images and principles behind them.</p>

caption of illustration too)?	
<p>Page 13 - 14 Exactly how La Borde could have been used as a natural trap could be more clearly explained and illustrated - the reader is rather left to take the authors (and excavators) suggestion that there is an aven that was used as a pit trap on trust. Where is the site in relation to the slopes? How steep is the slope? The cross-section given actually makes the landscape look very flat.</p>	<p>The explanation that the site is an aven is given on page 10, where it is explained that the archaeology was found in sediments filling a karstic depression. Our reasoning has now also been more clearly explained in the caption and page 14. The slope is about 1:10 gradient, which has been added to the text.</p>